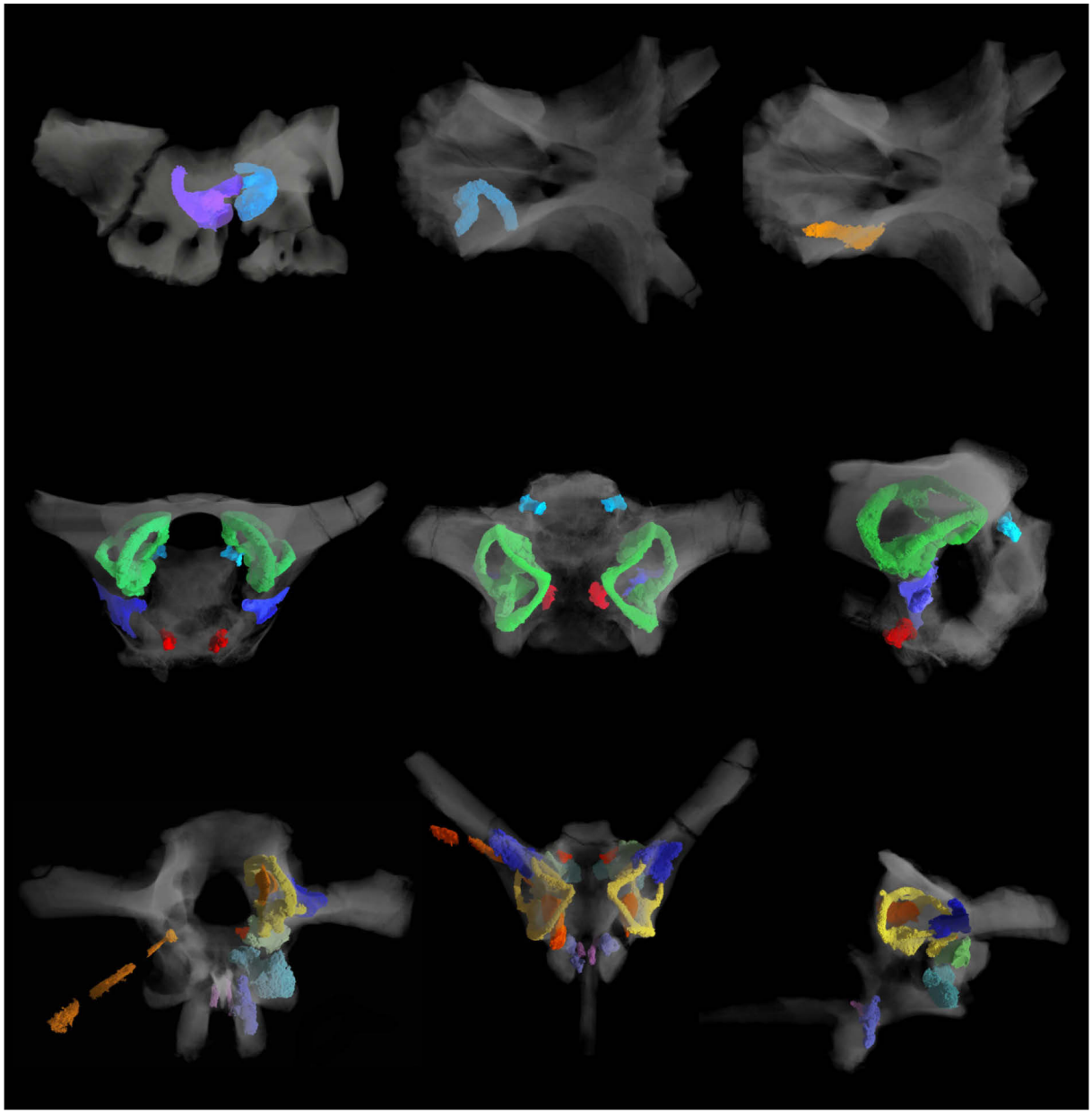
HUMBOLDT–UNIVERSITÄT ZU BERLIN

THE EVOLUTIONARY ORIGINS OF IMPEDANCE-MATCHING HEARING IN ARCHOSAURIA



GABRIELA SOBRAL

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THE EVOLUTIONARY ORIGINS OF IMPEDANCE-MATCHING HEARING IN ARCHOSAURIA

D I S S E R T A T I O N

Zur Erlangung des akademischen Grades

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von

MSc. Gabriela Barbosa Sobral de Oliveira

Präsident der Humboldt–Universität zu Berlin

Prof. Dr. Jan-Hendrik Olbertz

Dekan der Lebenswissenschaftlichen Fakultät

Prof. Dr. Richard Lucius

Gutachter: Prof. Dr. Johannes Müller

Prof. Dr. Jörg Fröbisch

Prof. Dr. Richard Butler

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“We live in every moment but this one
Why don’t we recognise the faces loving us so?
….
It’s hard to light a candle, easy to curse the dark instead”
(Last Ride of the Day, Nightwish)

“I wish none of this had happened.”
“So do I. And so do all who live to see such times. But that is not for them to decide. All we have to decide is what to do with the time that is given us.”
(Frodo Baggins and Gandalf, The Lord of the Rings: The Fellowship of the Ring)

ACKNOWLEDGMENTS

Once upon a time, there was an Elf who took the decision to enter a ship and cross the Big Blue. At the time, it was an easy, natural decision to make, for all her life had converged to that point. But she had forgotten the most primary rule of life: to every action there is always opposed and equal reaction. And looking always ahead, and unafraid of the unknown, she did not take notice of the pain that would come from what she had left behind, and from what she carried within. And nothing could have prepared her for this.

It is a dangerous business leaving your front door. Entering the land of the Bears seemed to be like dying but being still alive – or was it? When the sky pours, where to look for shelter? The swamp was full of dirty mud. Words made no sense, food had no taste. Who are you? What makes us so different and at the same time so similar? What parts of us do we need to change to adapt? What parts of us do we want to change? What do you do when you look in the mirror and cannot recognise yourself, when you think you have lost your muchness? At first, what seemed to be a simple pursuit of her dear dreams, revealed itself to be the darkest, most lonely journey she had even taken – to the deepest of her soul. For more than the challenges we face, the real meaning of such journeys often lies within – in the dreams we believe in, the people we love and the things we take for granted. How do you fight your demons? How do you face the fact that the things you hate, that make you unhappy, are actually reflections of your own failures and limitations? The times when the burden was just too heavy to carry were the times she was faced with her deepest fears – the old and the new, at the same time. Nobody told her it was easy, but no one ever said it would be this hard. When you do not care where to go, it does not matter which path to take. She felt like a stranger in a strange land, but she did not know that it is only after we have lost everything that we are free to do anything. The things she lost, the things she could not share. She found out everybody hurts and everybody cries, sometimes. And that we must hold on to all that is dear to us because we live as we dream – alone.

But it is only a passing thing, this shadow; even darkness must pass. The grey rain curtain rolls back and all turns to silver glass. And then you see it: white shores, and beyond, a far green country under a swift sunrise. Folk in the great stories had lots of chances of turning back, only they did not. They kept going because they were holding on to something. Without you, says the song, the poetry within me is dead. For the Elf, the poetry within does not even come to being if it is not to spend her time out of Valinor doing what she has done until now. Every warrior has the right to die in the battlefield he chose to live. And exactly this, all these challenges, this wandering life, the unknown… this is what the Elf chose for herself. The nightingale in the golden cage will soon be able to escape into the beauty of this ride ahead – such an incredible high.

~ ** ~

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[story of your life: time of solitude and strife,
freedom of an open road, hope, and many miles to go]

"How do you pick up the threads of an old life? How do you go on when, in your heart, you begin to understand there is no going back?
(Frodo, The Lord of the Rings: The Return of the King)

"Every little memory resting calm in me
Resting in a dream, smiling back at me
The faces of the past keep calling me to come back home"
(Rest Calm, Nightwish)

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ABSTRACT IN ENGLISH

Impedance-matching hearing is considered an important refinement of the auditory system of tetrapods because it reduces energy loss during sound transmission. Anatomically, it is characterized by the sub-division of the metotic foramen into a posterior vagus foramen and an anterior fenestra pseudorotunda. Impedance-matching hearing has evolved independently in several tetrapod groups including archosaurs and although it has been suggested that it represents a homoplasy, this hypothesis has never been tested. Therefore, 17 braincase characters were coded for 111 taxa and mapped on an informal supertree. Optimization of the characters revealed that the fenestra pseudorotunda appeared eight times independently in Archosauria, with five reversals. While this character is plastic in dinosaurs, it appeared only once in pseudosuchians. A tree-shape analysis revealed that pseudosuchians had six shifts in diversification rates, while dinosaurs had seven. Of these, only ornithischian ones are correlated to the appearance of impedance-matching hearing. Many of the overall state changes occur at the origin of major dinosaurian clades, but for pseudosuchians they are concentrated prior to the origin of Crocodyliformes and at the origin of Notosuchia and Thalattosuchia. The overall number of correspondences between character state changes and shifts in diversification rates is higher for dinosaurs, whereas in Pseudosuchia only Mesoeucrocodylia has a similar amount. It is thus possible to conclude that impedance-matching hearing is not homologous for archosaurs, and that it cannot be considered a key innovation triggering diversification. However, it may have played some role in ornithischian diversification. In general, the braincase anatomy of dinosaurs is more plastic than that of pseudosuchians. The abutting of the pterygo-quadrate complex against the lateral braincase wall was a strong anatomical constraint for crocodyliforms broken only by notosuchians and thalatosuchians.

KEYWORDS: Archosauria, braincase, middle ear, impedance-matching hearing, diversification rates, key innovation.

ABSTRACT IN GERMAN

Das impedanzwandelnde Hören ist eine wichtige Verfeinerung des Gehörsystems der Tetrapoden indem es einen Energieverlust während der Schallübertragung vermeidet. Anatomisch ist es durch eine Unterteilung des Foramen Metoticum in eine vordere Fenestra Pseudorotunda und ein hinteres Vagus Foramen charakterisiert. Dieses System trat mehrmals unabhängig in Amniota auf, und obwohl schon vorher vermutet wurde, dass es eine Homoplasie für Archosauria darstellt, wurde diese Hypothese bisher noch nicht geprüft. Demnach wurden 17 Hirnschädel Merkmale für 111 Taxa kodiert und auf einem informellen Supertrees optimiert. Die Analyse ergab, dass die Fenestra Pseudorotunda unbhängig acht Mal in Archosauria auftrat, mit fünf Umkehrungen. Während dieses Merkmal plastisch für Dinosauria ist, es trat nur einmal in Pseudosuchia auf. Eine Tree Shape-Analyse ergab, dass sechs Verschiebungen in den Diversifizierungsraten in Pseudosuchia und sieben in Dinosauria zu finden sind, von denen nur die der Ornithischia mit der Fenestra Pseudorotunda in Beziehung stehen. Viele Zustandsveränderungen erfolgen an der Basis der Dinosauria aber bei Pseudosuchia sind diese vor der Entstehung der Crocodyliformes und an der Basis der Notosuchia und Thalattosuchia konzentriert. Die Korrelationen zwischen Zustandsveränderungen und Verschiebungen sind höher in Dinosauria, während bei Pseudosuchia nur Mesoeucrocodylia eine ähnliche Anzahl aufweist. Daraus folgt, dass das impedanzwandelnde Hören nicht homolog in Archosauria ist, und dass es nicht als Schlüsselinnovation zur Erklärung der Vielfalt betrachtet werden kann, obwohl es eine Rolle in der Diversifizierung der Ornithischia spielte. Insgesamt ist die Anatomie des Hirnschädels der Dinosauria plastischer als die der Pseudosuchia. Die Positionierung des Pterygoid-Quadratum-Komplexes an die Seitenwand des Hirnschädels in Crocodyliformes stellt eine anatomische Beschränkung dar, welche nur von Notosuchia und Thalattosuchia durchbrochen wurde.

SHLAGWÖRTER: Archosauria, Hirnschädel, Mittelohr, Impedanzwandelnde Hören, Verschiebungen in Diversifizierungsraten, Schlüsselinnovation.

INTRODUCTION

SOUND PROPAGATION

The transition from an aquatic to a terrestrial environment imposed several constraints on the functional anatomy of vertebrates, accounting for substantial changes in skull morphology and architecture with consequences on systems such as feeding and hearing (Downs *et al*. 2008). Sound transmission varies significantly between aquatic and aerial media, and therefore, so do the mechanisms for sound detection.

In an aquatic environment, sound radiates spherically from a source in longitudinal waves comprised of the oscillation of both pressure and particle displacement components. While pressure oscillation is uniformly related to the distance from the source (Figure 1A), particle displacement results in a near and a far field (Figure 1B), where decrease ratio in wave amplitude is lower close to the source and higher further away (Lombard & Hetherington 1993). Hair cells are the basic sensory receptors of the auditory system of vertebrates, and because they and the aquatic medium are structurally very similar, detection of the displacement component of a sound wave is impossible if all parts oscillate in phase. Therefore, hair cells must be subject to the differential density resulting from the arrangement of several otic structures that provide a low-impedance, confined, and directed pathway for the displacement of the sound wave (Coffin *et al*. 2004, Lombard & Hetherington 1993, Manley 1990). On the other hand, the detection of the pressure component must necessarily be mediated by a transducer, since hair cells are only displacement-sensitive. Transduction mechanisms require more dramatic modifications in the otic region as they are represented by systems with different densities connected by membranes, with and without the participation of mechanical levers (Lombard & Hetherington 1993).

In a terrestrial setting, the correlation between distances from the source and displacement and pressure amplitudes are reversed. The low-pressure environment of air makes pressure-detection more difficult further away from the source – but this same characteristic facilitates particle displacement (Figure 1C). However, the difference in densities between the body of a terrestrial animal and the surrounding air is so significant that almost all the acoustic energy is reflected on its surface, making detection of the pressure component of the sound wave a much more feasible alternative (Lewis & Fay 2004, Lombard & Hetherington 1993).

The strikingly different impedances between the external environment and the inner ear result in meaningful energy loss during sound transmission, and require mechanisms for equalization of wave amplitudes, amplification of signal and avoidance of distortions caused by the changes in frequencies (Lewis & Fay 2004, Manley 1990). Acoustic impedance can

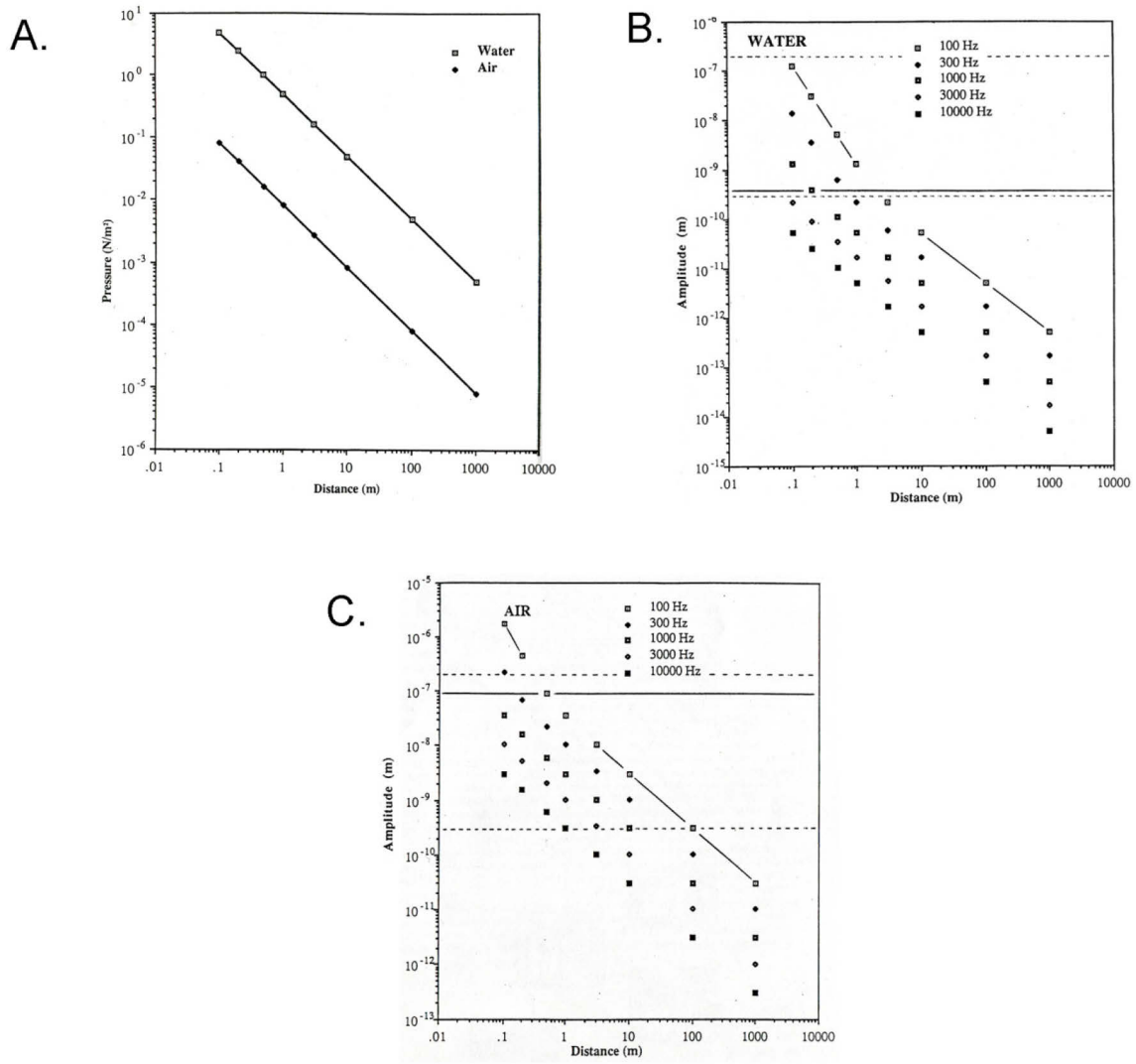

Figure 1: Idealized graphics depicting displacements in water and in the air. A) Pressure as a function of distance from the source for both air and water; B) Water particule displacement as a function of distance from the source. Dashed lines delimit the general sensitivity of range of a hair cell and the solid line represents the approximate boundary between near and far fields; C) Same as B but for air. Modified from Lombard & Hetherington 1993.

be defined as the resistance of the fluid of a given medium to be set into motion by sound wave propagation, given its physical properties. As stated above, the impedance of air is significantly lower than that of aquatic environments. The tympanic ear of tetrapods is both an acoustic pressure-displacement transducer and an impedance-matching device. It involves a complex system with a movable, exposed collector, the tympanum, connected to the otic capsule by a transducer, the stapes, in an air-filled chamber, the middle ear – or pharyngotympanic cavity (Lombard & Hetherington 1993, Manley 1990, Saunders *et al*. 2000).

THE TYMPANIC EAR

The tympanic ear (also referred to as a “modern” sense of hearing) has both a pressure-transducing and an impedance-matching function, as it involves a complex system of an external collector, a transducing lever, and an air-filled cavity. The tympanum is a convex, three-layer membrane superficially located in a frame formed by the quadrate anteriorly, the squamosal dorsally, the retroarticular process of the lower jaw ventrally, and soft tissue posteriorly (Wever 1978). It is connected to the stapes by a short, cartilaginous extra-stapes that bears four processes spreading onto the internal surface of the tympanic membrane (Figure 2A, B). The number of processes is usually four, but reductions to three or two are not uncommon, and in Iguanidae a fifth process is found. One or two ligaments help to fix the extra-stapes to the elements framing the membrane. A middle-ear muscle is present, the reflex of which reduces the sensitivity of the ear to loud sounds. The stapes is usually a thin rod with a cartilaginous coverage, whose distal-most part connects to the extra-stapes while its proximal footplate inserts into the fenestra ovalis, being kept firm by an annular ligament.

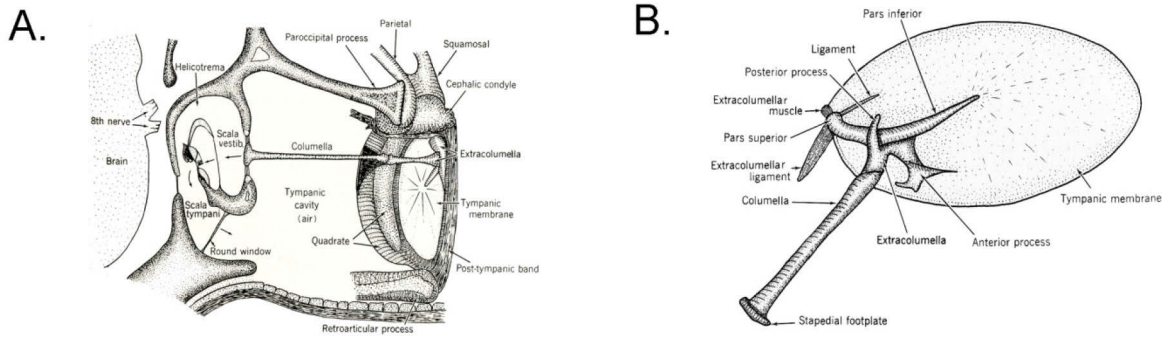

Figure 2: General morphology of the middle and inner ears of lizards. A) Right ear of *Sceloporus* in posterior view; B) Detail of right stapedial and extra-collumelar morphology of *Gekko*. From Wever 1978.

Being attached to the internal surface of the tympanic membrane and to the otic capsule, the stapes transmits motion caused by sound wave propagation into the fluids of the inner ear. By doing so, it transduces pressure into the displacement component detectable by the hair cells (Lombard & Hetherington 1993, Manley 1990). The tympanic ear also acts as an impedance-matching mechanism to compensate for energy loss during the acoustic reflection at the environment and tissue interface in two ways: the first is by amplification of the energy arriving at the body surface; the second is by the arrangement of the lever system involving the bony stapes and the cartilaginous extra-stapes (Lombard & Hetherington 1993, Manley 1990, Saunders *et al*. 2000). Amplification of the signal occurs because the tympanic

membrane has a large area for collection of sound relative to the footplate of the stapes that delivers it onto the fenestra ovalis. Amplification also occurs because the malleability and the curved form of the membrane enable it not to vibrate like a stiff plate, but to respond differently to stimulation across its surface. The arrangement of the lever system has an impact on the impedance-matching function of the ear by amplifying the motions of the tympanic membrane. The point of insertion of the extra-stapes on the tympanic membrane may alter its response to vibration. This leads to two different types (or classes or orders) of systems. A type 1, class I or first order, lever system (Figure 3A) is found in ranid frogs and in mammals (Jørgensen & Kanneworff 1998, Mason & Marr 2013, Mason & Narins 2002). Here, the fulcrum (the point of articulation between each element of the ossicle chain) is located between the place of the applied force (tympanic membrane) and the load (fluids of the inner ear). In almost all other tetrapods, the load is located between the fulcrum and the applied force (Figure 3B). This is accomplished by the extension of one process of the extra-stapes to the centre of the tympanum to receive the stimuli, while ligaments fix the system on the opposite end, at the edge of the membrane. The main body of the extra-stapes (which is connected to the inner ear and thus represents the load of the system) is inserted in the middle. This is called type 2, class II or second order lever system and is restricted to low-frequencies (Manley 1990). These mechanisms also reduce changes of frequency in wavelengths during sound transmission caused by the different impedances (Lombard *et al*. 1981, Hemilä *et al*. 1995, Kemp 2005).

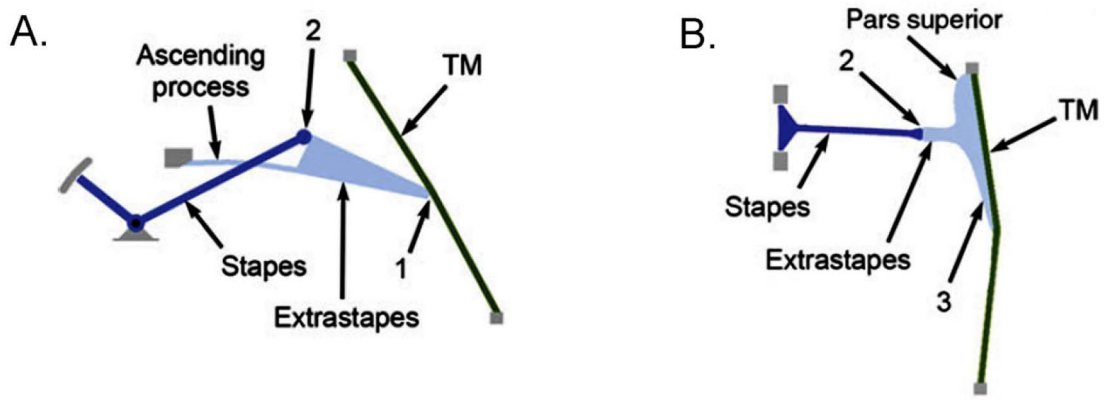

Figure 3: Different types of lever systems found in vertebrates. A) Type I, found in frogs; B) Type II, found in lizards. 1: attachment of extra-collumela to the tympanic membrane (TM); 2: articulation between stapes and extra-collumela; 3: pars inferior of reptile extra-columela. Modified from Mason & Marr 2013.

Due to its compressibility, the air filling of the middle ear cavity allows for movement of the tympanum in response to changes in sound pressure. The right and left cavities are connected to each other and to the pharynx through the eustachian tubes, equalizing the

pressure gradient within the system, and thus also acting as a directionally sensitive receptor. Other features of the middle ear cavity like volume and composition of its walls (such as by muscles, connective tissue, cartilage or bone) can heavily influence frequency response and thus play an important role in the hearing range. The degree of ossification, and thus flexibility, of the elements of the lever system and the middle ear cavity itself are responsible for the upper limit of the hearing frequency (Lombard & Hetherington 1993). At high frequencies, much of the energy is lost due to flexion of the system. Thus, ossification of the cavity and increased stiffness of the extra-stapes allow for the detection of higher frequency sounds. Although papillar development is connected to hearing sensitivity as well (as in longer organs populated with more hair cells), it alone is not responsible for the upper limit of the hearing range, which has been a further selective force for the ossification of the cavity in some clades.

The otic or auditory capsule lies on the posterior region of the braincase, lateral to the brain, and encloses the labyrinth. It is formed mainly by the prootic and opisthotic, with possible contributions from the supraoccipital and basioccipital. The main lateral opening of the otic capsule, usually covered by the footplate of the stapes, is the fenestra ovalis (also: oval window or fenestra vestibuli). Its anterior border is formed by the prootic and its posterior portion is formed by the opisthotic. The anterior ampulla lies within the prootic. From it, the anterior semicircular canal then extends dorso-postero-medially into the supraoccipital, while the lateral semicircular canal curves postero-laterally into the opisthotic, where the posterior ampulla is located. From there, the posterior semicircular canal runs dorso-antero-medially into the supraoccipital and to the common crus (also: recessus utriculi), where it meets the anterior semicircular canal. The cochlea lies between the prootic and opisthotic, but commonly partially excavates the dorso-lateral portion of the basioccipital. The labyrinth is formed by two distinct parts: the membranous (also: otic or endolymphatic) labyrinth and the osseous (also: periotic or perilymphatic) labyrinth. The following descriptions are based on Wever (1978) and Manley (1990), unless stated otherwise.

The Membranous Labyrinth: This part comprises ducts and sacs and is usually sub-divided into superior and inferior parts (Figure 4A). The superior division, also referred to as vestibular labyrinth or simply vestibule, includes the three semicircular canals surrounding the utriculum, and the endolymphatic duct and sac. Each semicircular canal is located at an approximately right angle relative to the other, roughly on each of the three planes of space (sagittal, coronal and transverse), and consists of a narrow duct that begins and ends in the utriculum. They bear bulbous expansions on each of their extremities, named ampullae. The anterior and posterior semicircular canals meet and together form the common crus, a larger duct that connects to the dorsal side of the utriculum. The utriculum consists of a main part

formed by a broad tube that runs from the common crus to the junction of the anterior and lateral ampullae, and by a sharply bent part confluent with the common crus that extends postero-ventrally, termed posterior sinus. The anterior region of the utriculum, adjacent to the junction of the ampullae, is called the utricular recess and contains a macular organ related to balance and head orientation, responding to sudden fluid displacements. The connection with the inferior division is made through a very narrow utriculo-saccular duct. The endolymphatic duct originates on the medial wall of the sacculus, running ventral to the main part of the utriculum and then dorsally, towards the cranial cavity through the endolymphatic foramen (housed usually by the prootic only, but in some cases also by the supraoccipital), where it expands and forms the endolymphatic sac. This sac can bear calcareous granules, sometimes in considerable amounts (Wever 1978, Manley 1995).

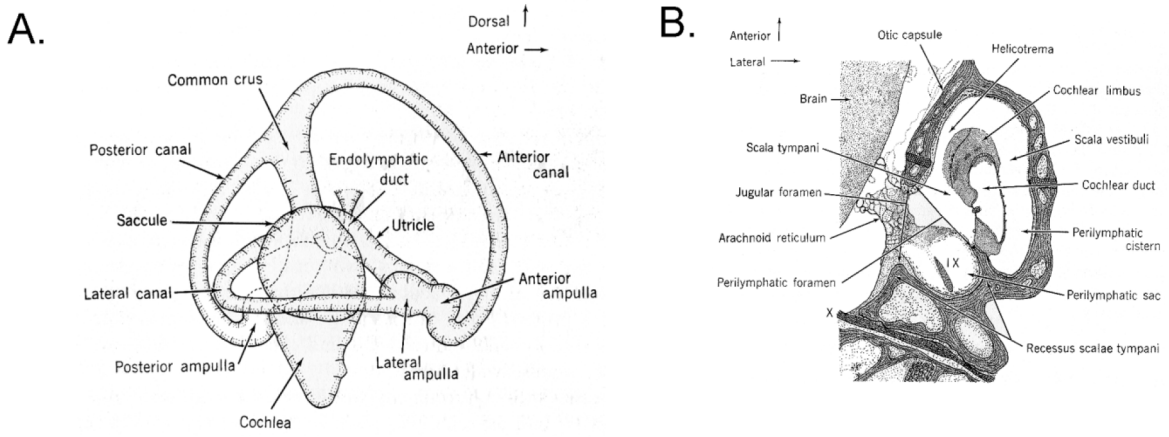

Figure 4: Structures of the inner ear of *Iguana*. A) Membranous labirynth; B) Transverse section of the right ear. Wever 1978.

The inferior division of the membranous labyrinth includes the sacculus and the cochlear duct. The macular organ of the sacculus occupies a big extent of its medial and ventral walls, and has a relatively big amount of statolistic mass. The sacculus connects to the cochlear duct through the sacculo-cochlear duct, whose size and position varies among species. In general, it is located at the postero-ventral extremity of the sacculus, extending ventrally and anteriorly. The cochlear duct of lizards is a chamber with the approximate form of an inverted pyramid and is usually divided into two distinct parts by the position of the limbic plate (part of the perilymphatic labyrinth – see below), the cochlea and the lagena, each containing sensorial organs: the auditory papilla and the lagenar macula, respectively. The auditory papilla occupies the posterior and dorsal portions of the duct, whereas the lagenar macula expands onto the anterior and ventral parts, sometimes reaching the postero-ventral part as well. Usually, the cochlea is more extensive than the lagena, but proportions between both parts vary considerably among taxa.

The membranous labyrinth contains eight labyrinth organs: three are macular organs (one in the utriculum, one in the sacculus and one in the lagena), three are crest organs (one in each of the ampullae of the semicircular canals), and the last two are known as papillae (one in the cochlea known as the auditory papilla and the other either on the utriculum wall or close to the common crus named the papilla neglecta). Of those, only the cochlear organ, the auditory papilla, is known to be an auditory organ, while all the others seem to be more related to balance, although the exact function of the macula lagena and of the papilla neglecta are still poorly understood. All these sense organs consists basically of hair cells, which respond either to movements of the statolistic mass or of the endolymphatic fluid – which in turn may correspond to sound transmission or to head movements.

The Perilymphatic Labyrinth: Despite its alternative name, osseous labyrinth, this part is not formed by bone, but consists of fluid-filled spaces and soft tissue networks that form plates and trabeculae. The perilymphatic labyrinth has a suspensory function, enclosing and maintaining the position of the epithelial structures of the membranous labyrinth. The most compact parts form plates – the most important of which is termed the limbo-cochlear plate – and offer a rigid support to those structures. These compact parts were referred to as cartilage by early anatomists, hence the alternative name, but histologically they bear no close relationships to this form of connective tissue. Instead, the terms bony, osseous or endosseous labyrinth are used in three-dimensional imaging papers to refer to anatomical correlates of braincase bones that surround inner ear structures (Witmer & Ridgely 2008a).

The spaces between trabeculae and plates result in a series of recesses and passageways that form the perilymphatic labyrinth in a more strict sense. The perilymphatic cistern is a large recess located medially to the proximal end of the stapes. Its anterior extension along the cochlear duct is known as the scala vestibuli (Figure 4B). The more medial region of the cistern is called the scalae tympani. A narrow passage, the helicotrema, connects both scalae. This structure plays an important role in pressure equalization during sound transmission (see below). A diverticulum of the perilymphatic system leaves the otic capsule posteriorly, bulging into an extracapsular, but also extracranial space – the recessus scalae tympani. This recess corresponds to a morphologically distinct region of the embryonic metotic fissure anterior to the passageway of cranial nerves IX – XI and the posterior cerebral vein. When leaving the capsule, the diverticulum is called the perilymphatic duct, the opening on the posterior wall of the otic capsule is the perilymphatic foramen (also called fenestra chochlea), and its bulging into the recessus region is called perilymphatic sac.

IMPEDANCE-MATCHING HEARING

Although the tympanic ear also has an impedance-matching function, further changes in the anatomy of the inner ear and on the braincase lateral wall account for an improvement of this function and for the appearance of so-called impedance-matching hearing (often times referred to as a “refined” sense of hearing). The two main morphological changes include the ossification of the medial braincase wall with the consequent structural separation of the inner ear from the rest of the brain, and the presence of a pressure-relief window (Manley 1990, Wever 1978). An unossified medial braincase wall allows for expansion movements of the inner ear structures and decreases the overall impedance of the system, facilitating sound transmission (Evans 2008). However, acoustic isolation hinders sound conduction along routes other than those where sound detecting tissues are located, maximizing the efficiency of the system (Lombard & Hetherington 1993).

Acoustic isolation without a compensatory mechanism can limit hearing capacity to low frequency ranges (Manley 1990, Wever 1978). Such a mechanism is represented by the appearance of a pressure-relief window. The metotic foramen is an opening on the lateral braincase wall through which the glossopharyngeal (CN IX), the vagus (CN X) and accessory (CN XI) cranial nerves, as well as the posterior cerebral vein, collectively leave the brain cavity (Gower & Walker 2002). When it becomes subdivided by a bony structure called the metotic strut, a vagus foramen is formed posteriorly usually carrying all the above mentioned elements and a fenestra pseudorotunda (apertura lateralis recessus scalae tympani, round window or fenestra cochlea – albeit incorrect, since it is not located on the cochlear recess and because this is also the name of the perilymphatic foramen) anteriorly (de Beer 1937, Rieppel 1985). The fenestra pseudorotunda is housed by the opisthotic, and the part separating the fenestra ovalis from the fenestra pseudorotunda is termed crista interfenestralis. The fenestra pseudorotunda is the lateral opening of the recessus scala tympani when it becomes delimited by the development of the metotic strut. The recess communicates medially with the brain cavity through the apertura medialis (also: perilymphatic aqueduct), being there in contact with the arachnoid membrane, and dorsally or anteriorly with the cochlear recess though the perilymphatic foramen. The membranes lining the middle ear cavity and the interior of the recessus scalae tymapni form the secondary tympanic membrane. Together, the fenestra and the membrane act as a pressure-relief device that further reduces acoustic impedance and thus avoids energy loss during sound transmission. It also reduces the movement amplitude of inner ear structures, protecting them from potential damage caused by overstimulation (Lombard & Hetherington 1993, Manley 1990, Wever 1978).

SOUND TRANSMISSION IN AMNIOTES

The basic sensory unit of the hearing system is the hair cell, which is derived from the lateral line of early vertebrates (Coffin *et al*. 2004). The transformation of its functional role from a basic receptor to the electrical and mechanical specializations found in the inner ear was heavily influenced by the environment in which the cells are placed, and depends on the surrounding fluids and tissues and on the degree of isolation from the external environment (Manley & Clack 2004). The hair cells are located in the cochlear duct, whose position is fundamental for sound stimulation. It lies between the stapedial footplate in the fenestra ovalis and the pathway leading to the fenestra pseudorotunda. In cases where the latter structure is absent, it lies nevertheless on the path of vibratory fluid flow (Manley 1990). The cochlear duct has five major tissue linings: the Reissner's membrane, the tectorial membrane, the basilar membrane, the auditory papilla and the lagenar macula (Wever 1978). Of these, only the auditory papilla and the basilar membrane are related to sound detection. The auditory papilla consists of a sensory structure made up of two cell types, hair cells and supporting cells. Most of the supporting cells rest on the thickened bottom part of the basilar membrane. However, in contrast to the other labyrinthine sensory organs, where hair cells are closely surrounded by supporting cells, in the auditory papilla they are largely free along their ventral parts. The basilar membrane is located transversal to the pathway of vibratory fluid that runs through the cochlea. When the fluid is set into motion by the stapedial footplate, the flexible basilar membrane is also caused to move, stimulating the cells of the sensory structures borne by it (Manley 1990).

There are two types of circuits that represent the two different stimulation processes for sound transmission in reptiles: the re-entrant fluid circuit and the pressure-relief system – with presence of the metotic foramen and of the fenestra pseudorotunda, respectively. The following descriptions are based on Wever (1978).

Re-entrant Fluid Circuit: The fluid passage of the inner ear leads from the internal boundary of the cochlea back to the lateral surface of the stapedial footplate in a circular path. When the fluid is displaced in a given direction, it involves not only the cochlear pathway but also the complete circuit back to the footplate (Figure 5A, B). A reversal motion of the footplate causes the entire circuit to move in reverse as well, setting up a churning movement in the system and causing the basilar membrane to react to the movements caused not only by the sound waves themselves, but also by the system going back to its initial position. At low frequencies, relatively less mass of the fluid must be displaced in order to transmit sound, but at higher frequencies, the mass is considerably greater. As a consequence, the impedance of the system increases with frequency, as its resistance due

to friction is correlated to the speed of motion – which varies according to the square of the frequency.

Anatomically, this circuit is related to the more basic tympanic ear type and to the absence of the fenestra pseudorotunda (see next chapter) – or, secondarily, to the relative immobility of the secondary tympanic membrane. It is therefore considered the plesiomorphic condition to amniotes (Clack & Allin 2004). As already mentioned, lack of ossification of the medial wall of the braincase allows for some movement of the inner ear structures into the brain cavity, decreasing the overall impedance of the system and facilitating sound transmission, thus playing a small compensatory role (Evans 2008).

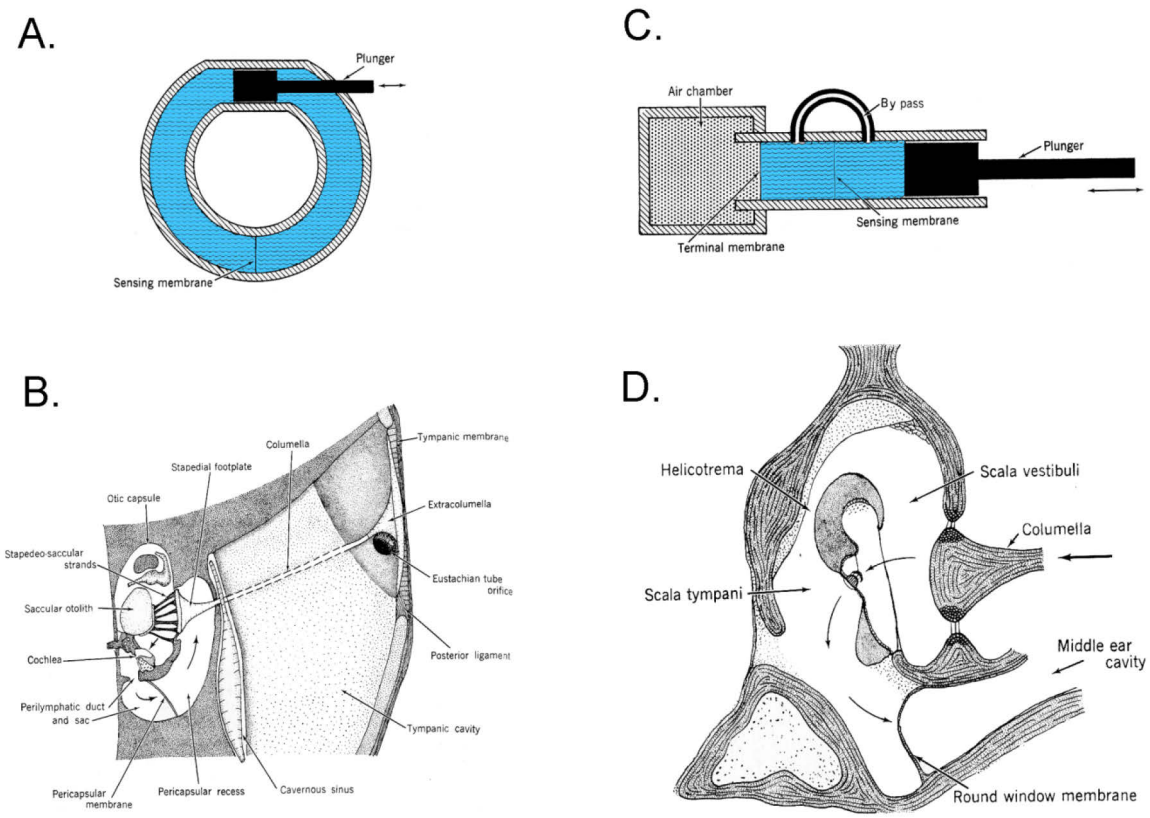

Figure 5: The two different types of sound transmission in amniotes. A) Schematic drawing of the Reentrant Fluid Circuit; B) The same in turtles; C) Schematic drawing of the Impedance-matching Hearing; D) The same in Iguana (transverse section). Arrows indicate fluid flow. Modified from Wever 1978.

Pressure-relief System: The course of fluid displacement runs from the stapedial footplate to the fenestra pseudorotunda through the cochlea only (Manley 1990). When pressure is exerted on the cochlear fluid, its displacement meets much less resistance because the flexible secondary tympanic membrane can protrude into the air cavity of the middle ear (Figure 5C, D). The higher mobility of the system decreases its impedance and extends the range of the auditory perception to high frequency tones. The presence of the

helicotrema also acts as a fluid pressure equalizer between the scala vestibule and the scala tympani. It prevents fluid accumulation resulting from stapedial movements on one of the sides of the basilar membrane that could otherwise distend or disrupt it. The presence of this structure slightly reduces the sensitivity of the system, but clearly compensates for the potential damage involved to the basilar membrane. As already noted, this pressure-relief system is related to the bony subdivision of the metotic foramen into a fenestra pseudorotunda anteriorly, which connects the posterior extension of the otic capsule, the recessus scalae tympani, to the middle ear cavity (see next chapter).

EVOLUTIONARY HISTORY OF THE VERTEBRATE HEARING SYSTEM

Unveiling the complex evolutionary history of the hearing system is a difficult task. Extant vertebrate groups may represent independent specializations that deviate significantly from a hypothesised plesiomorphic pattern (Manley & Clack 2004). On the other hand, following the timing of morphological changes in deep time depends on a good fossil record and robust phylogenetic hypotheses. In recent years, our understanding of the stepwise acquisition of characters as well as the interrelationships of vertebrate groups has been greatly modified and expanded by the description of intermediate taxa filling in gaps in our knowledge of cranial endoskeleton morphology (Brazeau & Ahlberg 2006, Clack 1998, Daeschler *et al*. 2006, Downs *et al*. 2008). The study of the evolution of the hearing system of vertebrates is not recent, and has been the subject of works of anatomists, physiologists, and palaeontologists alike (see Clack 2002, Fay & Popper 2000, Laurin 1998, Starck 1995). In pre-cladistic times, and following the theory of the evolution of species proposed by Darwin, the general line of thinking in the study of any biological system was to place the observed morphologies into a gradient that, in the particular case of vertebrates, would start with fishes and culminate in the anatomy of mammals (Fay & Popper 2000, Saunders *et al*. 2004). Due to the relationships of the inner ear structures to the surrounding bones of the otic capsule, hearing is one of the best documented functional transitions of sensory systems in the fossil record. However, as the fields of palaeontology and cladistics developed, placing the changes of the system along such a continuum proved to be impossible (Clack 2002, Saunders *et al*. 2004). Given this historical context, it is easy to understand the different proposed hypotheses for the evolution of the hearing system, which are as complex as the organisation of the ideas comprising the evolutionary history of tetrapods and their phylogenetic relationships.

The stapes is homologous among all tetrapods and evolutionarily derived from the hyomandibula (Figure 6A), the most prominent element of the hyoid arches and the second

of the branchial arches. The hyomandibula acts primarily in jaw suspension, and in fishes, for instance, it is involved in breathing and feeding (Kardong 2001). The plesiomorphic form of breathing in stem tetrapods (Figure 7) is suggested to have been similar to extant amphibians. As the pumping of air into the lungs through the mouth is made by the hyoid musculature, it is likely that the stapes retained a significant role in breathing in early tetrapods (Clack 2002). At some point, costal ventilation replaced mouth ventilation through the development of an intercostal musculature for inhaling and of an abdominal musculature for exhaling. The development of an alternative way of breathing broke the constraint imposed on the hyoid arch and musculature, freeing them up to act in other systems (Brainerd 1993, Clack 2002). Skull reorganization into a more solid structure due to constraints of terrestriality seems to have benefited from the decrease in the respiratory role of the stapes, which then gained an important bracing function (Figure 6B). In these cases, the stapes is a transversely oriented and still a rather stout element that contacts both the braincase and the skull roof (Clack & Allin 2004). This contact likely made possible the acquisition of a rudimentary hearing function, although stapedial morphology does not indicate an association with a tympanum (Clack 2002, Brazeau & Ahlberg 2008). Basal tetrapods were essentially aquatic and had a relatively simple, non-tympanic ear, and many taxa demonstrate the stepwise acquisition of characters, representing a less direct evolution of the hearing system of more terrestrial clades (Downs *et al*. 2008). The stapes is plesiomorphic, being very massive and retaining contact with the palate, but its footplate already has a contact with the fenestra vestibule (Clack 1998). The fenestra vestibuli is formed by several different bones of different embryologic origins (Figure 6C): dorsally it is formed by the prootic and opisthotic (cephalic mesoderm), anteriorly by the sphenethmoid or basisphenoid (neural crest), antero-ventrally by the parasphenoid (neural crest), postero-ventrally by the basioccipital and posteriorly by the exoccipital (both somitic mesoderm). However, the braincase is in general still poorly ossified, so questions related to other terrestrial adaptations such as the presence of a lagenar pouch or the existence of a perilymphatic foramen to compensate for auditory vibrations will likely remain unanswered (Clack & Allin 2004). More derived taxa also show palate openings, which might be associated with the buccal breathing that broke the functional constraint on the stapes.

Basal amniotes have a roughly similar otic morphology to the non-tymapnic ear of early tetrapods, lacking specific adaptations for terrestrial hearing. They possess a stout stapes directed slightly ventrally, strongly suggesting a retention in bracing function. The fenestra ovalis is also formed by many occipital arches and ventral braincase derived elements.

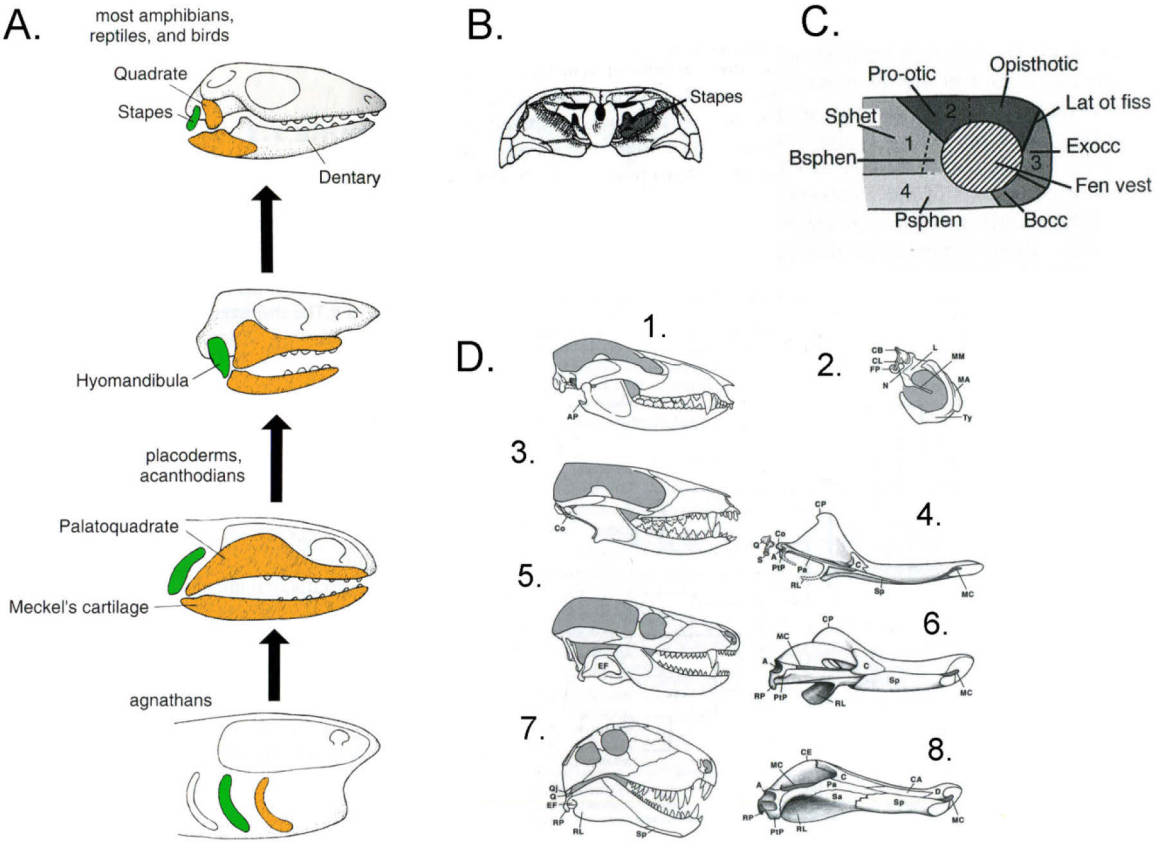

Figure 6: Evolutionary origins of middle ear structures. A) Homology of the hyomandibula (green) and mandibular arch (orange) – modified from Kardong 2001; B) bracing function of the stapes in the basal tetrapod *Geererpeton* – from Clack & Allin 2004; C) Diagram of the embryonic origins of the otic capsule in Devonian tetrapodomorphs. 1: sphenethmoid (sphet) and basisphenoid (bsphen), neural crest origin; 2: prootic and opisthotic, cephalic mesoderm origin; 3: exoccipital (exocc) e basioccipital (bocc), somatic mesoderm origin; 4: parasphenoid (psphen), dermal bone of neural crest origin. Fen vest: fenestra vestibuli; La ot fiss: lateral otic fissure; D) Evolution of the middle ear ossicles of synapsids. 1: *Didelphis*; 2: Tympanic annulus and middle ear of Didelphis (pars tensa of tympanum in grey) in lateral view; 3 and 4: *Morganucodon* skull and medial side of lower jaw; 5 and 6: *Procynosuchus* skull and medial side of lower jaw; 7 and 8: *Dimetrodon* skull and medial side of lower jaw. A: articular; AP: angular process of dentary; C: coronoid; CA: anterior coronoid; CB: crus breve of incus; CE: coronoid eminence; CL: crus longus of incus; Co: condyle of dentary; CP: coronoid process; D: dentary; EF: external fossa; FP: footplate of the stapes; L: lamina of malleus; MA: anterior process of malleus largely formed by the prearticular; MC: Meckel's cartilage; MM: manubrium of malleus; N: neck of malleus; Pa: prearticular; Ptp: process for the insertion of pterygoideus muscle (homologous to the tensor tympani); Q: quadrate (homologous to incus); QJ: quadratojugal; RP: retroarticular process of articular; RL: reflected lamina of angular; S: stapes; Sa: surangular; Sp: splenial; Ty: tympanic or ectotympanic. Modified from Clack & Allin 2004.

Figure 7: Simplified phylogeny of Tetrapodomorpha. Red arrows indicate the presence of a pressure-relief mechanism. Based on Bickelmann *et al*. 2009, Holland & Long 2009, Müller & Reisz 2006, and Marjanović & Laurin 2013.

Amniotes represent, however, the development of full terrestriality and show some further changes in skull structure and hearing system. The tympanic ear is characterised mainly by the thinning of the skin surface on the temporal region of the skull with the consequent appearance of a tympanum and by a complete loss of the bracing function of the stapes. This allowed it a central role in hearing, with the concomitant development of a long paraoccipital process and a reduction in size of the stapes, which freed it from its functional bracing role (Clack 2002). A connection to the tympanic membrane and a rotation to a more direct orientation between tympanum and inner ear through the stapes are further changes in the development of a tympanic ear (Clack & Allin 2004).

The hypothesis on the evolutionary origin of the tympanic ear that resisted the longest was the “early tympanum hypothesis” or the “standard view” (Laurin 1998, Lombard & Bolt 1979). According to this hypothesis, the tympanic ear, with a slender stapes and the presence of a middle ear cavity and a tympanic membrane, evolved early in tetrapod evolution, being thus homologous among all the different tetrapod clades. Back then, “labyrinthodontian” temnospondyls were the model group for basal amniotes in general which, despite possessing no otic notch and owing a massive stapes that articulated with the quadrate, were reconstructed as bearing a tympanic ear. Evidence from the different relationships between the chorda tympani branch of the facial nerve (CN VII) and the stapes, and the orientation of this bone in amphibians and amniotes, as well as the characteristic three ossicle chain of mammals that differs from all other tetrapods, dismissed this hypothesis (Lombard & Bolt 1979). New discoveries of basal labyrinthodonts and other tetrapods provided further evidence that an early tympanum was incorrect. In the light of comparative works on the soft anatomy of extant clades focusing on the topographical relationships of the chorda tympani with the different processes of the stapes, an “alternative view” was proposed (Lombard & Bolt 1979). According to it, a tympanic ear evolved independently in amphibians, mammals and reptiles, and was in agreement with the knowledge of the fossil record of the time. The main issue with this hypothesis concerned the monophyly, phylogenetic relationships and evolutionary history of extant amphibians, temnospondyls and amniotes, a problem that still persists and that has yet to be fully understood (Marjanović & Laurin 2013). The “new hypothesis” proposed by Laurin (1998) acknowledges the fact that the presence of an otic notch on the temporal region of the skull necessarily implies the presence of a tympanic membrane, and while it deals essentially with accounts of amphibian phylogeny, it also reinforces that a tympanic ear was absent in early amniotes. Although not yet fully resolved, the phylogenetic relationships of early tetrapods has changed drastically in the last two decades and has affected interpretations on character state evolution of terrestrial hearing as well (Clack & Allin 2004). Unfortunately, usage of three-dimensional imaging techniques such as computed tomography (CT) has not yet been

extensively applied to these groups and features of the middle and inner ears. Therefore, issues such as the degree of ossification between the otic capsule and braincase, the course of the perilymphatic system, size of the cochlear and vestibular parts of the inner ear, and existence and development of the eustachian tubes remain poorly understood.

The relatively early split between synapsids and reptiles in the late Carboniferous has led to analogous but fundamentally different hearing mechanisms (Clack & Allin 2004). Mammals have a rather well-documented transformation series on the evolution of the middle and inner ears (Prothero 2007), but that of reptiles remains poorly understood. For example, early in the evolutionary history of synapsids, mastication was the selective force shaping many of the modifications found in their skulls. With the development of increasingly powerful muscles, the dominance of a single and robust bone became advantageous to support the stress imposed upon the lower jaw by these muscles. In this sense, the presence of post- and paradentary bones in the lower jaw and the cranio-mandibular joint between the articular and quadrate were gradually replaced by the derived conformation found in extant mammals: the postdentary bones are lost or reduced, being incorporated into the ossicle chain or to other mechanisms of the middle ear, and a new cranio-mandibular joint is formed between the dentary and squamosal (Figure 6D – Clack & Allin 2004, Kardong 2001).

Another example of analogy between both groups is that capacities for sound discrimination have been achieved in different ways. Complex sounds are decomposed in discrete component frequencies, and therefore the auditory epithelium is tonotopically arranged along its axis – an organisation mediated by both mechanical and electrical mechanisms. In mammals, mechanical tuning plays a significant role in tonotopic discrimination. Different groups of hair cells have stereocilia with varying degrees of length and stiffness, and the mass of the basilar membrane itself changes topographically. Thus, different parts of the hearing organ resonate differently to the same sound frequency. In order to expand the hearing range, an increased number of cells is necessary, and the cochlea shows a tendency for elongation and coiling (Manley & Clack 2004). Due to a higher degree of ossification of the braincase in general, this anatomy is accurately reflected in the bones of the otic capsule and therefore registered in the fossil record. Reptiles on the other hand rely more extensively on physiological tuning mechanisms such as electrical resonance for sound discrimination. In these, hair cells set up a voltage gradient via active K^+/Ca^{2+} channels, oscillating in response to a depolarizing stimulus. The size and number of specializations involved in vesicle transport within and release from the cell is also important (Mann & Kelley 2010).

In basal groups of Reptilia (Figure 7), however, significant modifications start to appear independently in parareptiles and diapsids. The presence of distinct emarginations at the postero-lateral edge of the skull in derived parareptiles might suggest that they

possessed a tympanic membrane (Müller & Tsuji 2007). Furthermore, the paroccipital process is well developed, reaching the skull roof, and the fenestra ovalis is small and restricted to the prootic and opisthotic bones. They also seem to have possessed an impedance-matching hearing ear, with the presence of a fenestra pseudorotunda and the complete ossification of the braincase medial wall. Basal taxa of Reptilia such as *Captorhinus* and *Araeoceslis* have no otic notch on their temporal regions (Figure 8B). The stapes is massive, ventrally positioned and contacts the quadrate which, together with a short paroccipital process, suggests that it still retained a major bracing function (Heaton 1979, Reisz 1981). Basal diapsids, on the other hand, represented by *Youngina*, have a more developed paroccipital process contacting the quadrate and a relatively more slender stapes, although still rather massive (Figure 8C). In addition, the latter still contacted the suspensorium laterally, but an ossified extra-stapes is present. The quadrate possessed no otic notch and provides no evidence for the presence of a middle ear cavity, and the basioccipital does not take part in forming the ventral rim of the fenestra ovalis (Evans 1987, Gardner *et al*. 2010). There is currently no consensus on the presence of a tympanic ear in diapsids mainly due to lack of fossils, although the anatomy of *Youngina* indicates a step-wise acquisition of the middle ear morphology in basal diapsids. Therefore, a better understanding of the general braincase anatomy and phylogenetic relationships of these groups is still urgently needed.

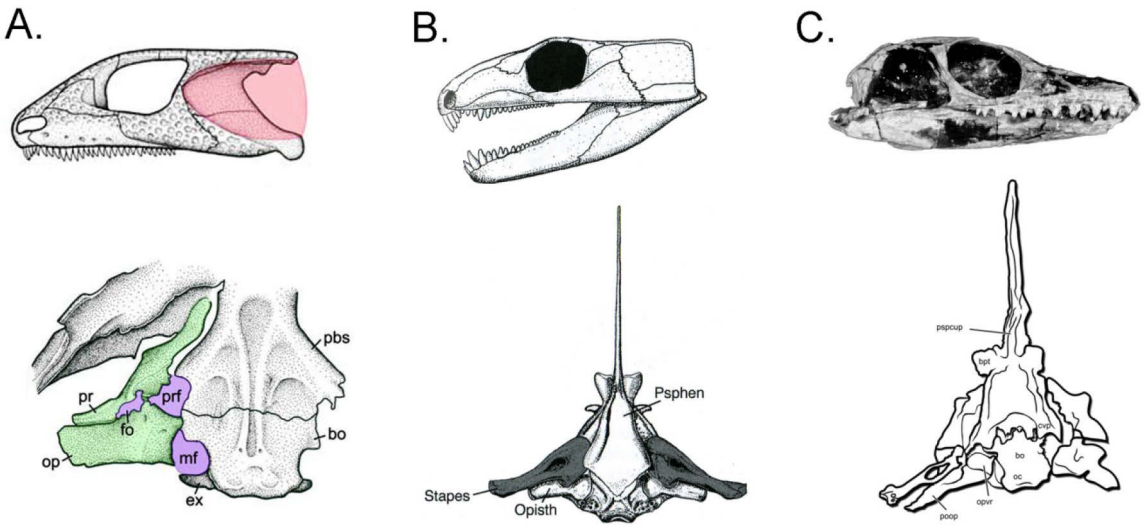

Figure 8: Lateral skull and ventral braincase views of basal reptiles. A) *Bashkyroleter* (Parareptilia – Müller & Tsuji 2007); B) *Captorhinus* (Eureptilia – Clack & Allin 2004); C) *Youngina* (Diapsida – Gardner *et al*. 2010). ex: exoccipital; bo: basioccipital; bpt: basipterygoid process; cvp: crista ventrolateralis process of the parasphenoid; mf: metotic fissure; fo: fenestra ovalis; oc: occipital condyle; Opisth. Opisthotic; opvr: ventral ramus of the opisthotic; pbs: parabasisphenoid; poop: paroccpital process of opisthotic; pr: prootic; prf: pressure-relief window; pspcup: cultriform process of parasphenoid; Psphen: parasphenoid.

ARCHOSAURIA

Archosauria is currently defined as the crown-group including all descendants of the most recent common ancestor of avialans and crocodilians (Figure 7 – Nesbitt 2011). The group appeared during the Early Triassic, but it was not until the Late Cretaceous that crown diversification events took place. In contrast with saurian origins, the understanding on the anatomy, paleobiology and phylogenetic relationships of basal archosaurs, as well as more derived closely-related archosauriform clades, increased substantially in the last two decades (Nesbitt *et al*. 2013). Current archosaurian phylogenetic, ecological and morphological diversity represent only a minor subset of the total diversity achieved during the long evolutionary history of the group (Brusatte *et al*. 2010b).

Since squamates have historically been the model system for reptiles, the anatomy and development of their otic region and capsule is fairly well understood (de Beer 1937, Gaupp 1900, Oelrich 1956). While the tympanic ear *per se* was not such a debated issue in this group, the subdivision of the metotic foramen and thus the appearance of impedance-matching hearing had its phylogenetic importance noted by the end of the last century. Its non-homology among saurian groups was evident and the non-homology of the fenestra between avialans and crocodilians was suggested (Gauthier *et al*. 1988, Bellairs & Kamal 1981, Gower & Weber 1998, Rieppel 1985, Whetstone & Martin 1979). However, in contrast to early tetrapods and lepidosaurs, the otic region of archosauromorphs has been largely neglected, even in more derived clades. Because crocodilians were classically seen as nothing more than a super-sized lizard, and because avialans were thought to be strongly morphologically constrained by flight and to stand “outside the main stem of vertebrate descent” (Gray 1908), relatively little anatomical work has been done in both groups. To be fair, the entire field of anatomy has experienced a major decrease in interest from researchers and the general public alike for most of last century; a scenario that is fortunately starting to change with the increased pace of technological developments and their affordability (Hutchinson, 2014). For these reasons, the general morphological pattern described in the previous section is largely based on squamates, as historically studies on reptile anatomy have been based on them (de Beer 1937, Gaupp 1900, Manley & Clack 2004, Wever 1978).

The middle ear of basal archosauromorphs seems to have been tympanic, although without anatomical indications as clear as those found in basal lepidosauromorphs. Thus, it may be that the presence of a tympanic ear is homologous for both groups (Clack & Allin 2004). Detailed braincase descriptions exist only for a limited number of taxa. The braincase of *Prolacerta* was thoroughly described by Evans (1986), but a discussion contextualizing the evolution of the archosauriform braincase was better approached by Gower & Weber (1998) in the description of *Euparkeria*. The basal archosauriform *Erythrosuchus* was described by

Gower (1997) and Gower and Sennikov (1996), which also included *Vjushkovia* and the poposauroid pseudosuchian *Xilousuchus*, but a more detailed discussion was only provided by Gower (2002), Gower & Nesbitt (2006) and Gower & Walker (2002) while describing *Batrachotomus*, *Arizonasaurus* and *Stagonolepis robertsoni*, respectively. A detailed description is also available for *S. olenkae* (Sulej 2010). The work of Walker (1990) on *Sphenosuchus* still remains the best documentation of a basal crocodylomoprh, followed by a thorough comparative discussion on braincase morphology. A recent approach by Pol *et al*. (2013) on the evolution of crocodylomorphs with the description of *Almadasuchus*, while not focusing on the otic region, also offers an insight on the mechanisms underlying braincase anatomy modifications with regards to its akinetic nature. The work of Kley *et al*. (2010) also offers a good source of anatomical information on crocodylomorph braincase anatomy, in particular for notosuchians.

Although the skull of crocodilians follows rather closely the plesiomrophic archosaur pattern, their braincase is strikingly divergent. The increased role of the lower jaw and corresponding muscles are the main driving forces to shape crocodilian skull anatomy, whose main characteristic is the strengthening of the palato-quadrate complex to the braincase (Starck 1979, Pol *et al*. 2013). The basioccpital of crocodilians is shifted so that in posterior view it forms a vertical plate ventral to the occipital condyle, where usually the openings of the eustachian system can be seen (Figure 9A). As a consequence, the braincase floor forms a perpendicular angle with the lateral semicircular canal, and has led de Beer (1937) to incorrectly state that this canal was vertical instead of horizontal. The paraoccipital process is also much developed and, together with the posteriorly rotated latero-posterior surface of the fused exoccipital and opithotic, further encloses the occipital region of the skull and delimits the middle ear cavity posteriorly (Iordansky 1973). Because of this feature, elements leaving the braincase such as the hypoglossal and vagus nerves do so posteriorly, instead of laterally. The extensive contacts of the basisphenoid with the quadrate and pterygoid are mostly responsible for the akinetic nature of crocodilian braincase, and this complex basically delimits the middle ear cavity ventrally. The braincase anterior wall is ossified, enclosed by the laterosphenoids, which also has an extensive contact with the quadrate, together forming the anterior wall of the middle ear cavity. Because of this arrangement, the middle ear cavity lies deep within the skull, and communicates with the external ear through a long channel formed by the quadrate (Iordansky 1973, Wever 1978).

The tympanic membrane of crocodilians is mostly supported by the quadrate, covered by a pair of earlid muscles that protect it when the animal submerges (Wever 1978, Saunders *et al*. 2000). The fenestra pseudorotunda is directed laterally and located ventro-posteriorly to the fenestra ovalis, so the cochlear and vestibular parts of the inner ear are

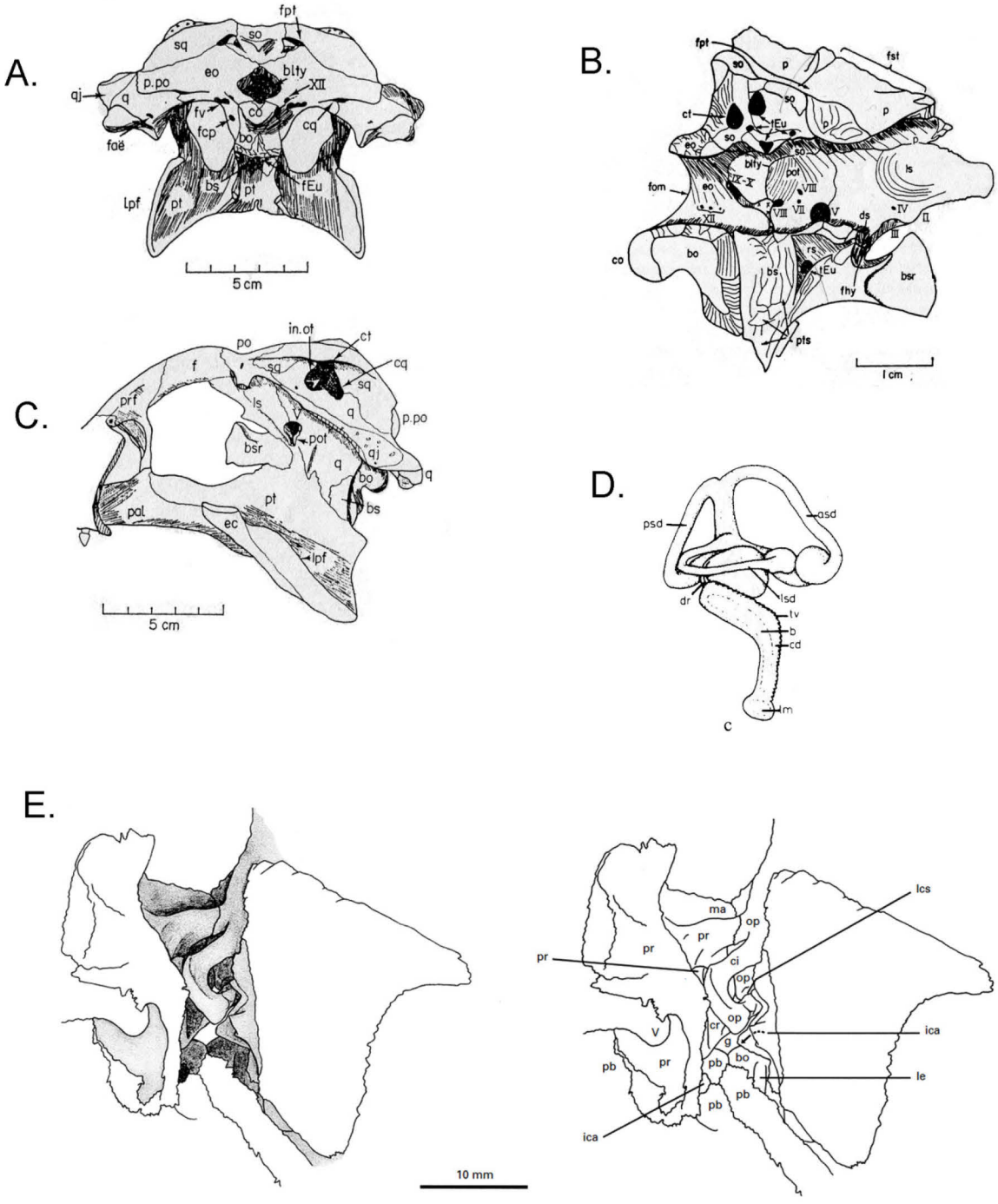

Figure 9: Braincase anatomy of extant crocodilians. A) Posterior view of *Caiman*; B) Left medial view of *Alligator*; C) Left lateral view of *Caiman*; D) Generalized crocodilian inner ear; E) Left middle ear of *Crocodylus*. asd: anterior semicircular canal; b: basilar papilla; blty: bulla tymapni; bo: basioccpital; bs: basisphenoid; bsr: basisphenoid rostrum; cd: cochlear duct; ci: crista interfenestralis; co: occipital condyle; cq: cranio-quadrate passage; cr: cochlear recess; ct: transverse canal; dr: sacculo-cochlear duct; ec: ectopterygoid; eo: exoccipital; ds: dorsum sella; f: frontal; faë: foramen aerium; fcp: posterior carotid foramen; fEu: Eustachian tube foramen; fom: foramen magnum; fhy: hypophyseal fossa; fpt: post-temporal fenestra; fv: foramen vagus; ica: internal carotid artery; in.ot: incisura otica; g: gap; Lpt: lateral flange of pterygoid; lcs: loop closure suture; le: lateral Eustachian tube; lm: lagena macula; ls: laterosphenoid; lsd: lateral semicircular canal; ma: mastoid antrum; op: opisthotic; p: parietal; pal: palatine; pb: parabasisphenoid; pot: prootic; po: post-orbital; p.po: paroccipital process;

also positioned in this manner, deviating slightly from the lepidosaurian pattern (Figure 9E). While the cochlear duct of lepidosaurs is triangular in shape (therefore also called the pyramid), the duct of crocodilians is tube-like and somewhat elongate and bent at about its mid-portion (Figure 9D), dividing the auditory papilla into dorsal and ventral portions, being commonly superficially compared to the coiled mammalian cochlea (Gray 1908, Wever 1978). The perilympahtic foramen is also very characteristic, as it opens laterally instead of posteriorly, just dorsal to the fenestra pseudorotunda, and does not transmit the perilymphatic duct (de Beer 1937).

On the other side of archosaur phylogeny, very little is known for pterosaurs. Other than for *Scaphognathus* (Newton 1888) and for *Tapejara* and *Anhanguera* (Kellner 1996), braincase descriptions virtually do not exist. While pterosaurs were initially also in the scope of this study, there have been technical delays which prevented the data collected to be added in time for a more complete discussion. The braincase morphology of dinosaurs is comparatively better explored. While the works of Janensch (1935, 1936) serve as the base for a number of more recent descriptions, some of his statements must be taken with care and need to be updated, as lack of proper discrimination between literature references and personal observations, as well as misinterpretation of anatomical information, has compromised parts of his contributions. More recent publications can be regarded as better sources of anatomical information such as Balanoff *et al*. (2010) on the description of *Apatosaurus*, Galton (1974) on *Hypsilophodon*, Sampson & Witmer (2007) on *Majungasaurus*, Witmer & Ridgely (2009, 2010) on tyrannosaurs and Witmer *et al*. (2008) on *Camarasaurus* and *Diplodocus*.

The general skull anatomy of avialans is extremely modified from the plesiomorphic archosaurian condition, and seems to have been influenced by the relative enlargement of the eyes and the corresponding development of areas of the brain and of the vestibular system, as well as the reduction of the role of the lower jaw for prey capture (Starck 1979). Instead of being located laterally, the otic capsule of avialans lies slightly ventral to the brain (Figure 10A, B). Therefore the tympanic frame is composed of the basitemporal plate antero-ventrally, the exoccipital posteriorly, and the squamosal and quadrate antero-dorsally – the latter two elements being connected to the stapes by an extra ligament (Starck 1995). Also, because of this rotation, the anterior region of the capsule, where the foramen of the facial

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pr: prootic; prf: pre-frontal; pt: pterygoid; psd: posterior semicircular canal; pts: sutural surface for articulation with pterygoid; q: quadrate; qj: quadratojugal; rs: rhomboid sinus; s: squamosal; so: supraoccipital; tEu: Eustachian tube; tv: tegumentum vasculosum. Roman numerals II–XII: corresponding cranial nerves. A–C from Iordansky 1973, D from Manley 1990, and E from Gower & Weber 1998.

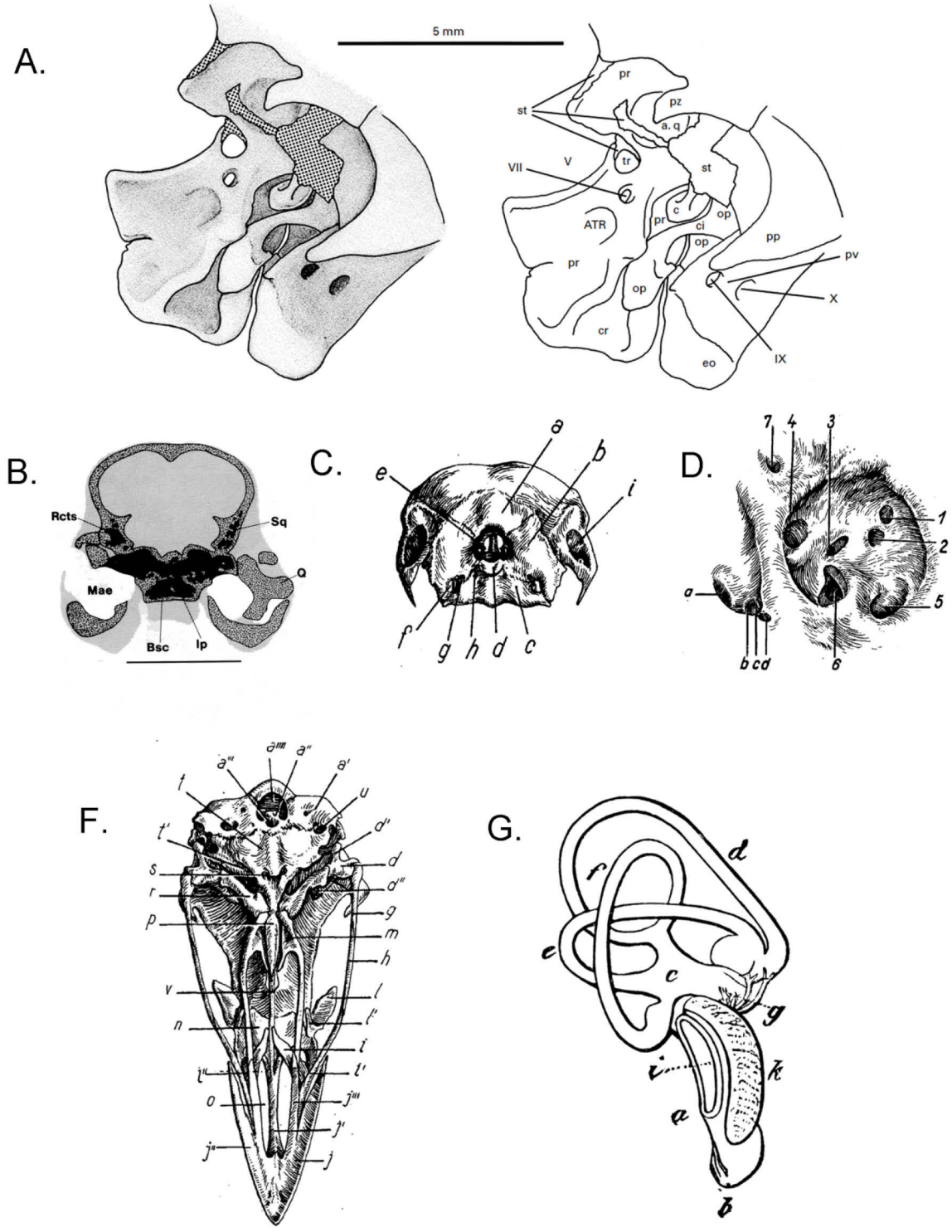

Figure 10: Braincase anatomy of extant avialans. A) Lateral braincase wall of *Somateria*; B) Coronal section of braincase and otic capsule of *Rhea*; C) Posterior view of the skull of *Meleagris*. a: supraoccipital; b: exoccipital; c: basioccpital; d: occipital condyle; e: foramen magnum; f: carotid and jugular foramen; g: vagus foramen; h: hypoglossal foramen; i: orbital process; D) Left medial view of the braincase of *Meleagris*. 1: foramen for the anterior branch of the auditory nerve (CN VIII); 2. foramen for the posterior branch of the CN VII; 3: foramen for the saccular branch of the CN VIII; 4: foramen for the posterior ampullar branch of the CN VIII; 5: foramen

nerve is found, has shifted dorsally (Figure 10C, F), while the posterior region of the lateral braincase wall is shifted posteriorly as in crocodilians (Bolk *et al*. 1936, Gray 1908). The degree of ossification of the middle ear cavity is also higher than in the remaining of diapsids (Figure 10D). In addition to the braincase dorso-medially and the temporal region dorso-laterally, the paroccipital process and part of the ossified metotic cartilage form the occipital wall, a vertical plate that delimits the middle ear cavity posteriorly (Figure 10E). The basitemporal plate is a compound structure formed mainly by the parabasisphenoid that bounds the cavity ventro-medially, while anteriorly it is enclosed by the parasphenoid-derived alaparasphenoid (Starck 1995, Witmer 1990). The basitemporal plate encloses the proximal part of the large eustachian tubes that connect the middle ear to the buccal cavity. Most neognathous avialans possess a paratympanic organ on the medial wall of the middle ear cavity. This organ is a small, elongate vesicle embedded in connective tissue whose mechanosensory epithelium consists of hair cells (O'neill *et al*. 2012). Although its exact function remains debated, the paratympanic organ is suggested to have a barometric and altimetric role by sensing changes in air pressure at the tympanic membrane and may be related to the spiracular sense organ of fishes (Giannessia *et al*. 2013). Since a functional organ is found in post-embryonic stages only in avialans and juvenile crocodilians and a vestigial one in a few non-avian vertebrate embryos, it is considered an ancestral amniote character retainend or re-evolved in avialans and lost in most of other amniote groups (von Bartheld & Giannessi 2011).

The hearing system of avialans is also highly specialised (Figure 9G). The vestibular part of the labyrinth is much reduced, while the cochlear duct is extended and, although not coiled, it is somewhat curved. In addition, part of the cochlea is more vascularised than

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for the facial nerve; 6: foramen for the cochlear and lagenar banches of CN VIII; 7: perilimphatic foramen; a: vagus foramen; b: glossopharyngeal foramen; c: foramen for anastomic ramus of the glossopharyngeal nerve; d: cochlear foramen; F) Ventral view of the skull of *Meleagris*. a': exoccipital; a'': occipital condyle; a''': subcondylar fossa; a'''' - foramen magnum; d: quadrate; d': otic process of quadrate; d'': orbital process of quadrate; g: quadratojugal; h: jugal; i: nasal process of maxilla; i': zygomatic process of maxilla; i'': palatine process of maxilla; j: premaxilla; j': frontal process of premaxilla; j'': maxilar process of premaxilla; j''': palatine process of premaxilla; l: lacrimal; l': orbital process; m: palatine; n: nasal; o: nares; p: presphenoid; r: pterygoid; s: Eustachian tube foramen; t: basisphenoid; t': alisphenoid; u: carotid and jugular foramen; v: vomer; G) Schematic drawing of the right inner ear of *Haliaetus*. a: cochlea; b: lagena; c: vestibule; g: utricle; d: anterior semicircular canal; e: lateral semicircular canal; f: posterior semicircular canal; h: utriculo-saccular duct; k: scala vestibuli; i: fenestra pseudorotunda. Other abbreviations: ATR: anterior tympanic recess; Bsc: basisphenoid complex; c: stapes; ci: crista interfenestralis; cr: cochlear recess; Ip: interaural pathway Mae: meatus acusticus externus; op: opistothic; pp: proccipital process; pr: prootic; pv: pre-vagal strut; pz: zigmatic process of squamosal; Q: quadrate; Rcts: recessus scalae tympani; Sq: squamosal; st: soft tissue; tr: tympanic recess. Roman numerals: corresponding cranial nerves. A from Gower & Weber 1998, B from Starck 1995, C–F from Gheţie 1976, G from Coues 1884.

those of lepidosaurs (Gray 1908). The semicircular canals radii of curvature are enlarged, and therefore they do not closely surround it, but are located farther away. The anterior semicircular canal is extremely elongate, although the length and inclination when leaving and re-entering the vestibule vary among different clades. It surrounds a very well developed fossa subarcuata, and in many groups its corresponding ampulla does not communicate with the lateral ampulla of the lateral semicircular canal (Bolk *et al*. 1936). The utricle is much larger than the saccule and contains enlarged otoliths. The perilymphatic duct and sac (the former also referred to as cochlear aqueduct), as well as the recessus scalae timpani (also peirlymphatic recess), have a constant morphology in the group, although their topography and size may very slightly (Gray 1908).

DIVERSIFICATION

How clades diversify is one of the central questions in macroevolutionary studies – how selective forces shape anatomies and capacities, allowing groups to occupy spaces and times and become a significant part of their ecosystems. With over 10,000 avialan species, archosaurs are the most diverse clade of extant tetrapods (Benson & Choiniere 2013) – a story that began with the origin of the group after one of the most significant mass extinction events in Earth history at the Permo-Triassic boundary. Non-avian dinosaurs are one of the most studied groups of extinct vertebrates, and their origin, dominance in terrestrial Mesozoic faunas, and sudden extinction at the Cretaceous-Paleogene boundary has been subject of intense research (Brusatte *et al*. 2010a, Upchurch *et al*. 2011). The processes and patterns underlying dinosaur radiation has experienced an increased amount of interest in the past years, with the development of several refined analytical methods for estimating diversity (Barrett *et al*. 2009, Brusatte *et al*. 2008a; 2010a; 2012, Irmis 2010, Lloyd *et al*. 2008, Upchurch *et al*. 2011, Wang & Dodson 2006). However, taxic diversity is but one mean to explore the radiation of a given group, as many components are often involved, and sometimes in an independent way: morphological disparity, rates of discrete morphological changes and evolutionary rates of continuous characters have recently gained ground. For instance, body size has been a well explored proxy for assessing rates of evolution in archosaurs. It is often regarded as a fundamental trait in vertebrate biology, as it closely relates to ecological, physiological and life-history characters (Sookias *et al*. 2012). Most of these topics are, however, still surveyed in isolation, with few attempts to integrate these data in order to evaluate if they are correlated or not.

Several hypotheses have been suggested to try to explain the radiation of dinosaurs, especially based on competition with other groups. For example, it had been hypothesized that the extinction of non-crocodylomorph pseudosuchians could have allowed the opportunistic takeover of early dinosaurs. However, dinsoaurs were experiencing intense

taxic and morphological diversification while supposedly competing groups were still around, and their extinction had no impact in rates of taxonomic and morphological diversification (Brusatte *et al*. 2008, 2010a, 2010b). On the other hand, key innovations are traits usually regarded as being responsible for differentiated diversification, which may drive the exceptional radiation of some groups. Herbivory had been suggested as a key innovation for non-avian dinosaurs, but it was shown to be linked only to the early high rates of diversification of sauropodomorphs (Barrett *et al*. 2010). Refinement of the hearing system has been suggested to coincide with the origin of some insect groups, although the exact "otic specializations" were not specified (Clack 1997). In Clack (1997), the appearance of the fenstra pseudorotunda is assumed to be connected to the appearance of the tympanic membrane, making "tympanic hearing" a synonym to "impedance-matching hearing". However, although many squamate groups showing a loss of the pressure-relief window also show a loss of the tympanum, this association is not supported, as explained above. Because archosaurs (avialans in particular) and mammals are the amniote groups known to most heavily rely on sound for intraspecific communication, it is hypothesized that the development of an impedance-matching mechanism could be regarded as a key innovation for archsoaurs.

OBJECTIVES

Many of the examples mentioned above have focused on anatomical descriptions of braincases, although some also extend the discussion to the evolutionary history of several structures and behaviours. Very few of these have, however, focused strictly on the otic region, so that the homologous nature of certain archosaurian characters remain speculative. When discussing the phylogenetic relationships of extant avialans with "thecodonts", Gower & Weber (1998) provided a thorough anatomical and nomenclatural revision on the metotic foramen and fenestra pseudorotunda of basal archosaurs. It became clear that the nomenclature introduced by de Beer (1937) in an attempt to clarify the analogy between the reptilian and mammalian structures was ironically misleading as, in contrast to what had been alleged (Whetstone & Martin 1979), evidence suggested the fenestra pseudorotunda of avialans and crocodilians might not be secondarily homologous. This was however not studied in depth, and the hypothesis was never properly tested. Therefore, the present thesis is an attempt to compile the available information on the archosaur braincase to test the hypothesis of secondary homology of impedance-matching hearing.

SPECIFIC GOALS

- Provide suplementary information on the braincase anatomy of early archosauriforms, helping to build a more complete and coherent scenario on middle ear evolution;
- Test weather impedance-matching hearing represents a homoplasy or a homology for Archosauria and, if not, assess how often it has evolved in the group and when it first appeared, documenting the anatomical diversity observed;
- Verify if impedance-matching hearing can be regarded as a key innovation triggering the phylogenetic diversification of archosaurs;
- Interpret results in the context of the evolution of Mezosoic terrestrial vertebrate ecosystems.

BRAINCASE ANATOMY

In order to understand the evolution of the middle and inner ears of fossil archosaurs, it is necessary to understand the relationships of the otic capsule with the remnant of the braincase, for this is the only way to assess these informations in the fossil record and to propose homologies. As mentioned in the previous chapter, good braincase descriptions exist for some archosaur taxa, but they are unfortunately still patchy and do not form a coherent framework of archosaur morphology to be used in interpretations of braincase evolution. During the course of this study, the opportunity to conduct computed tomography scanning of two important archosauromorph braincases, belonging to *Mesosuchus* and *Euparkeria*, appeared. As closely related groups of Archosauria, they help building a more concise framework of archosaur morphological evolution and are therefore included here. Taxa will be described in a phylogenetic manner, from the more basal to the more derived clade. With execption of *Dysalotosaurus*, which has already been published, these descriptions will feature future publications of their own, in the context of archosauromoph braincase and inner ear evolution.

Archosauromorpha is one of the clades composing Sauria (Figure 7), and is thought to have originated in the Late Permian (Ezcurra *et al*. 2014). The phylogenetic relationships of early members of this clade have been subject of several studies, but these remain controversial (Dilkes 1998, Müller 2004). The first specimen described, *Mesosuchus browni*, belongs to the Rhynchosauria. These were first thought to be closely related to the extant rhynchocephalians, but where later referred to archosauromorphs along with other closely related taxa generally called “prolacertiforms” (Dilkes 1998). Although their exact position within the group varies slightly, they are regarded as derived taxa close to Archosauriformes. This latter group also originated in the Late Permian, but became diverse during the Triassic, becoming an important part of Mezosoic terrestrial ecosystems (Sookias *et al*. 2014). In this scenario, *Euparkeria* plays an important historical role in depicting the early evolutionary history of archosaurs. It is often regarded as being very closely related to the group, and has thus been used as morphological and biogeographical model for the origin of archosaurs. *Dysalotosaurus*, on the other hand, is a much more derived archosaur from the Late Jurassic of Tanzania. As an ornithopod dinosaur and sister group of most other Iguandontia, it offers a good amount of information on early ornithopod braincase evolution.

MORPHOLOGICAL ANALYSIS

Selecting and analysing the morphological characters related to the neuroanatomy of archosaurs is not trivial because the information available in the literature is patchy and very often incomplete. In palaeontology, the issue is overlooked not only due to the complexity of the subject itself, but also to problems inherent of the field such as incompleteness of the material, bad preservation or lack of preparation of the region of interest. Relying on literature

descriptions of fossil braincases was, for most cases, not possible. If materials themselves are rare, detailed works are generally absent. Perceptions of crocodilians as "generalised" or "primitive" have influenced interpretations of their anatomy and impeded advancements in several fields of knowledge of the group. I feel the anatomical survey has particularly affected them – and this problem was not detected early enough during the course of this project. However, performing such a study, although feasible, falls outside of the scope of this work. Anatomical information for crocodilians is urgently needed.

First-hand analysis of selected material was performed and, when possible, specimens were CT scanned. Scans were performed at the Museum für Naturkunde Berlin using a Phoenix|x-ray Nanotom tomography machine (GE Sensing and Inspection Technologies GmbH, Wunstorf, Germany). Being specifically designed for small-sized samples, it allows for a higher resolution in the visualization of small structures. Scans comprised 1440 slices, and were made with a tungsten target using a 0.1 mm thick Cu filter in modus 0, averaging 3, and skip 2. Slices were then reconstructed using the datos|x-reconstruction software, version 1.5.0.22 (GE Sensing and Inspection Technologies GmbH, Phoenix|x-ray) and the resulting volume was segmented and analysed in VG Studio Max 2.1 (Volume Graphics, Heidelberg, Germany).

RYHNCHOSAURIA

Early rhynchosaur studies made extensive comparisons with *Sphenodon*, assuming its close relationships with rhynchocephalians. It was only much later that rhynchosaurs were reassigned to Archosauromorpha, along with “Prolacertiformes” (Dilkes, 1998). Since then, analyses have repeatedly recovered rhynchosaurs as more closely related to archosaurs than to lepidosaurs, and subsequent debate has focused on the relationships of Rhynchosauria to other archosauromorph clades. It is sometimes found to be closer to Archosauriformes than “prolacertiforms” (Bickelmann *et al*. 2009, Müller 2004, Ezcurra *et al*. 2014), but a more basal position has also been retrieved (Jalil 1997, Rieppel *et al*. 2003, Senter 2004, Renesto & Binelli 2006). However, the phylogenetic relationships of basal saurians remain problematic due to several methodological issues (Sobral et al. *in prep*).

MESOSUCHUS BROWNI

The Middle Triassic *Mesosuchus browni* from the *Cynognathus* Assemblage Zone of South Africa was first described as a “rhynchocephaloid” (Broom 1913), playing a major role on the discussion of the origin of lizards (Broom 1925). The material SAM-PK-6536 was scanned with exposure time of 1000ms, 80kV, current of 450μA, and voxel size of 27.08μm.

Braincase: The braincase is displaced postero-ventrally, so that its anterior portion is visible in dorsal view (Figure 11A, D). The basioccipital is a short bone when compared to more derived archosauromorph clades (Figure 11B; 12A, B). It contributes a small part to the ventral rim of the foramen magnum and to the floor of the foramen of CN XII. The occipital condyle has a slightly inverted-triangle shape with very soft vertices and does not protrude too markedly from the braincase. Just anterior to the condyle, occupying most of its ventral surface, the basioccipital shows a low, curved rim whose concavity faces anteriorly. This rim connects the bases of the left and right basal tubera, to which the basioccipital contributes only to its posterior surface. There are two open areas filled with matrix a short distance anterior to this rim (Figure 12B), between the basioccipital and the basisphenoid, but only on the right side does it represent the suture line separating both elements, as confirmed by the CT scans. The real suture runs around the postero-medial border of the bases of the tubera. It is difficult to follow it on its most medial part because the bones are dorso-ventrally thin and the suture is largely interdigitating. The suture follows a short way antero-medially, meeting in the midline while describing a smooth arch which is posteriorly concave. On the right side the basiocciptal has no contribution to the foramen of the pneumatic sinus. However, on the left side it seems to contribute to part of the posterior border of it (see below).

The basisphenoid is elongate and forms most of the braincase floor (Figure 11B; 12A, B). Its ventral surface is also concave, so that the whole ventral surface of the braincase floor is depressed. The bone is narrower anteriorly. It has a waist at around its anterior third and flares posteriorly to form the external surface of the basal tubera. They are well-marked and projected posteriorly, with both anterior and posterior surfaces somewhat flattened, with a marked ridge separating them. The suture with the opisthotic was not found, but given the conformation of these structures in the CT scans (see below), it is assumed the basisphenoid does not contribute to the ventral border of the fenestra ovalis. The basipterygoid processes are prominent and directed ventrally and slightly anteriorly (Figure 13C). The external foramina for the internal carotid arteries are located close to the midline and lie posterior to the bases of the basipterygoid processes (Figure 12B; 13A, C). They run antero-dorsally and open on the dorsal surface of the basisphenoid, on the floor of the hypophyseal fossa. The fossa is relatively shallow, as its lateral borders are lower than the dorsal margin of the cultriform process. The middle part of the dorsum sellae is missing and its remaining lateral portions are narrow and connect to the ventral rim of the foramen of the CN V (Figure 11D; 12C). A subtle ridge runs antero-posteriorly in the midline of the hypophyseal fossa, sub-dividing it in two. Neither a foramen nor a pathway for the CN VI was found. A suture between para- and basisphenoid could not be identified with confidence, but a V-shaped interruption found at the base of the cultriform process between the vidian canals could

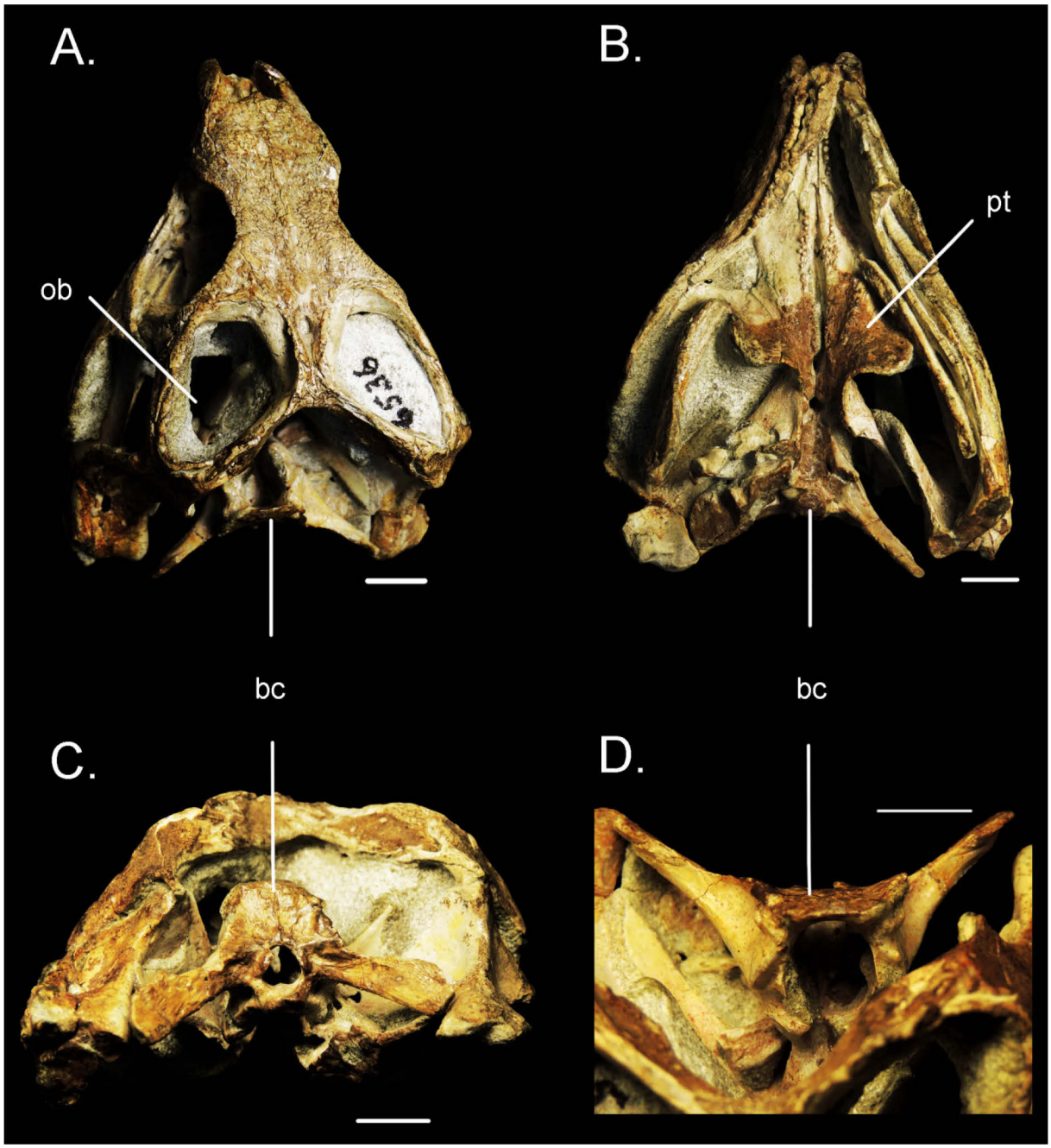

Figure 11: Skull of *Mesosuchus browni* SAM-PK-6536. A) Dorsal view; B) Ventral view; C) Posterior view; D) Detail of the braincase. bc: braincase; ob: orbit; pt: pterygoid. Scale bars equal 1cm.

indicate their contact. In this case, the parasphenoid would be restricted to the cultriform process only. The cultriform process is fairly long and possesses a sulcus running along its dorsal surface, which is more marked proximally.

The prootic is notched anteriorly, forming all but the antero-dorsal rim of the foramen of the CN V (Figure 11D; 12C, 13C). On the posterior rim of the foramen, the prootic is depressed, indicating the position of the gasserian ganglion. It is not possible to discern between the paths of the V_1 and V_{2+3} branches of the trigeminal nerve, although the antero-

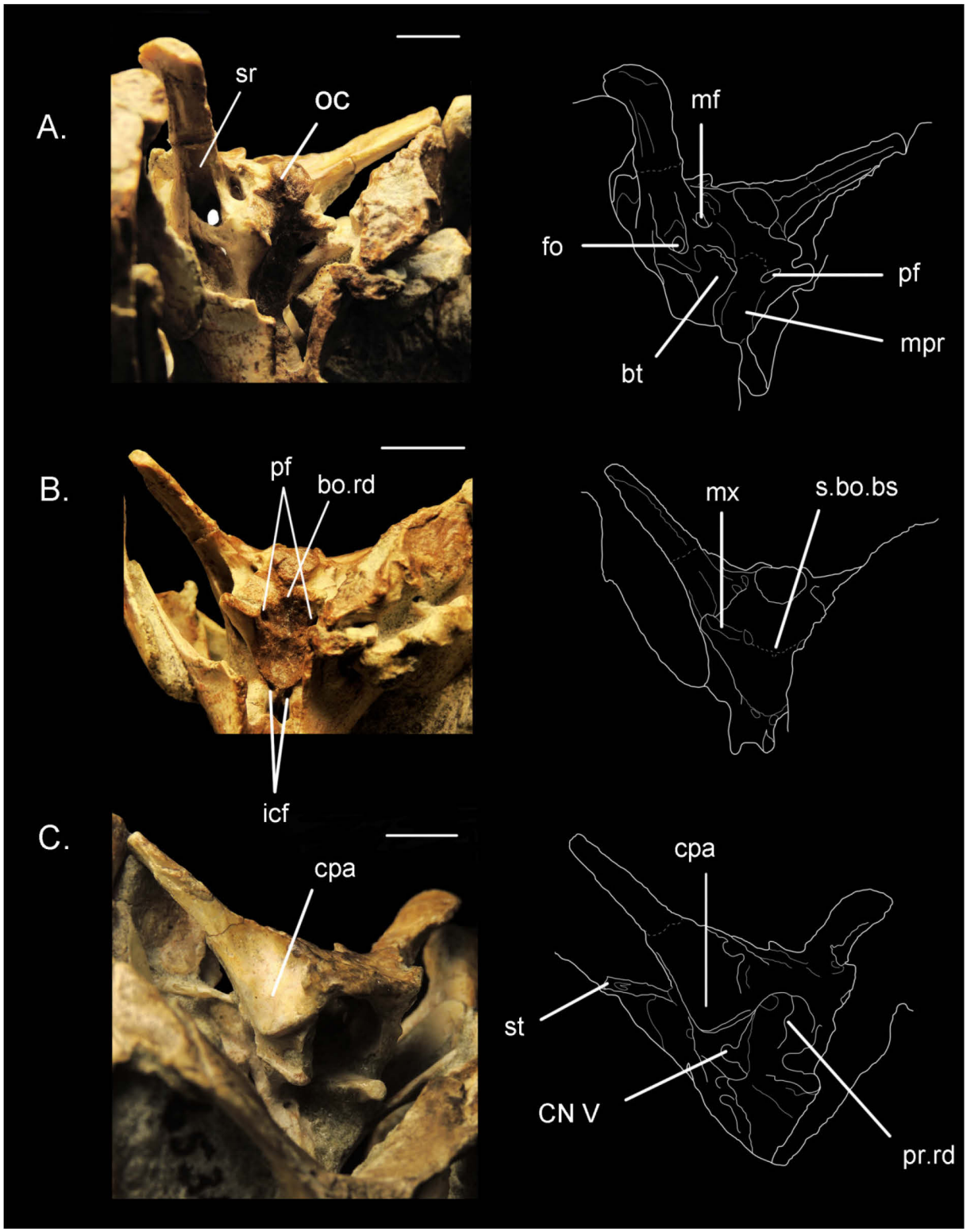

Figure 12: Braincase of *Mesosuchus*. A) Left latero-ventral view; B) Ventral view; C) Right latero-anterior view. bt: basal tuber; cpa: crista parotica; CN V: foramen of the trigeminal nerve; fo: fenestra ovalis; icf: internal carotid foramen; mf: metotic foramen; mpr: medial pharyngeal recess; mx: matrix; oc: occipital condyle; pf: pneumatic foramen; pr.rd: prootic ridge; s.bo.bs: suture between basioccpital and basisphenoid; sr: stapedial recess; st: stapes. Scale bars equal 1 cm.

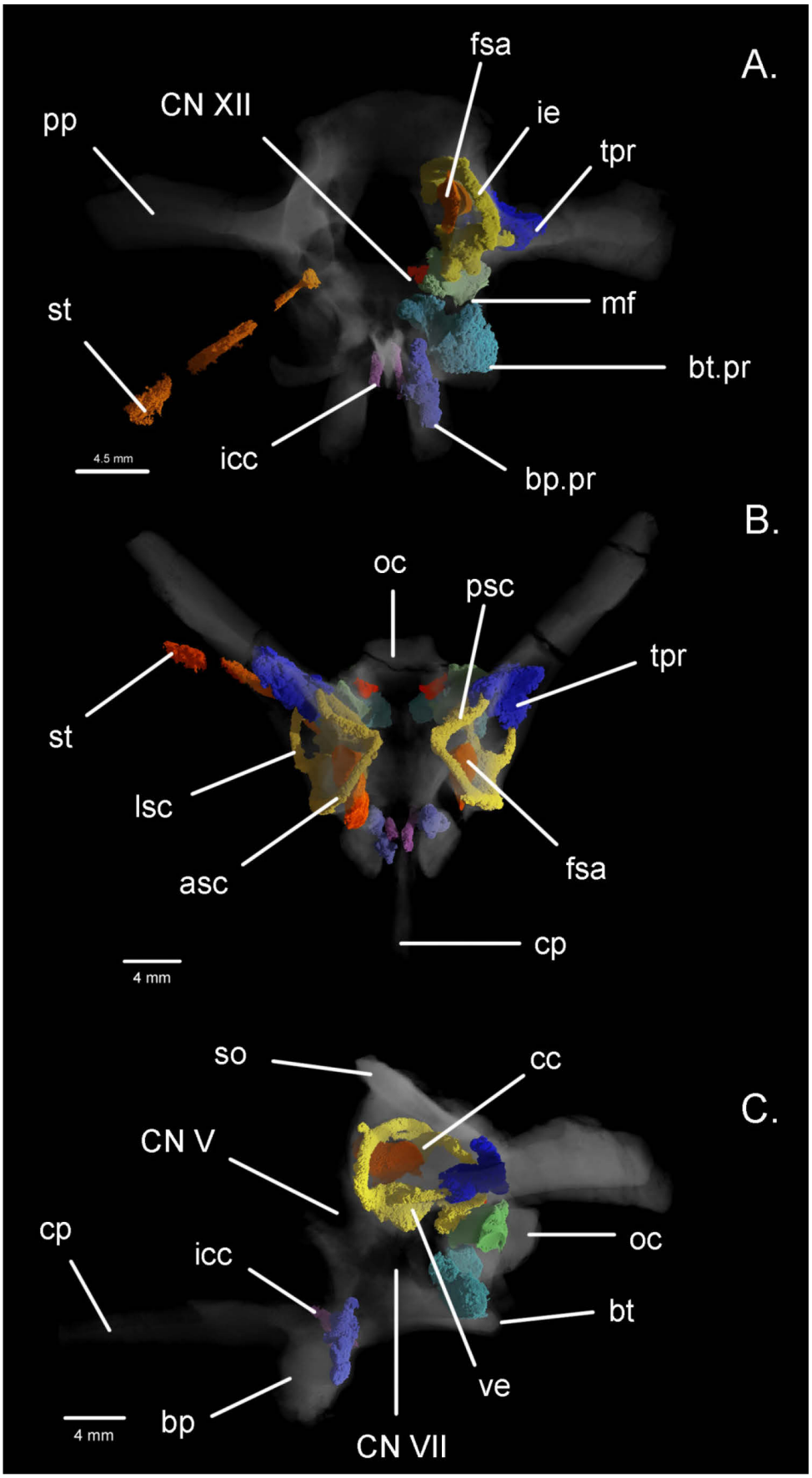

Figure 13: CT scans of the braincase and inner ear of *Mesosuchus*. A) Anterior view; B) Dorsal view; C) Left

dorsal base of the basipterygoid process bears a smoothly concave depression that could represent the course of the maxillo-mandibular ramus. Laterally, the crista parotica is strongly pronounced, dividing the prootic into anterior and posterior surfaces, where the foramina for the trigeminal and facial nerves are found, respectively. The crista parotica is connected to the paroccipital process by the crista prootica, which is obliquely positioned dorsal to the foramen of the facial nerve (Figure 12C). It begins distally on the antero-ventral surface of the paroccipital process, runs proximally, and bends antro-ventrally on the prootic. It then swings shaprly antero-dorsally to the anterior region of the braincase. At this point, the crista parotica connects to it ventrally, just posterior to the foramen for the CN V. The crista parotica runs around the posterior border of the CN V and continues ventrally onto the posterior border of the basipterygoid process. The lateral surface of the prootic, dorsal to the crista prootica, is smooth and depressed. On the left side, the foramen of the CN VII is damaged giving it an enlarged appearance (Figure 13C). One branch of the CN VII seems to have run dorso-posteriorly ventrally to the crista prootica and the other ran ventrally, posterior to the crista parotica and the basipterygoid process. On the posterior border of the CN VII, another strong crista runs dorso-ventrally and separates the foramen of the CN VII from the fenestra ovalis, for which the prootic contributes to the anterior border. The development of the cristae parotica and prootica, as well as the anterior border of the fenestra ovalis creates a deep recess on the lateral surface of the prootic where the foramen of the CN VII is located. This extends a short distance onto the lateral surface of the basisphenoid. On the medial wall of the prootic, it is possible to see the much enlarged fossa subarcuata. Like in *Euparkeria*, it seems to enter into the bone. However, CT scans reveal that, on the right side, the fossa is covered with matrix. The postero-ventral border of the fossa projects prominently medially.

The opisthotic forms for the posterior region of the lateral wall of the braincase. Its suture lines with the exoccipital are observable (see below), but the suture lines with the prootic or supraoccipital could be found. The opisthotic likely forms the paroccipital process entirely, except for the proximal third of the ridge formed by the crista prootica. The processes are very long and antero-posteriorly flattened, with the anterior surface facing ventrally. Their ventral rim is straight, but the dorsal ones flare distally at the tip of the processes. They are strongly directed dorsally and posteriorly, at approximate angles of 45°

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lateral view. asc: anterior semicircular canal; bt.pr: pneumatic recess of the basal tuber; bp: basipterygoid process; bp.pr: pneumatic recess of the basipterygoid process; cc: common crus; cp: cultriform process; CN V: foramen of the trigeminal nerve; CN VII: foramen of the facial nerve; CN XII: canal of the hypoglossal nerve; fsa: fossa subarcuata; icc: internal carotid canal; ie: inner ear; lsc: lateral semicircular canal; mf: metotic foramen; oc: occipital condyle; pp: paroccipital process; psc: posterior semicircular canal; tpr: tympanic recess; so: supraoccipital; st: stapes; ve: vestibule.

(Figure 11–13). They lie on the same level of the foramen magnum. Both processes are broken proximally close to their mid-length. The antero-ventral surface of the paroccipital process is deeply and extensively excavated by the recessus stapedialis (Figure 12A). The ventral ramus of the opishotic is thick and forms not only the crista interfenestralis separating the fenestra ovalis from the foramen magnum, but also a good part of the braincase floor in this region, including the ventral part of the fenestra ovalis – and thus also the basal tubera internally. The crista interfenestralis runs from a postero-dorsal to an antero-ventral position.

The exoccipital forms the posterior wall of the metotic foramen, most of the foramen of the CN XII and the lateral border of the foramen magnum. Part of the suture between exoccipital and opisthitic runs antero-posteriorly, dorsal to the metotic foramen and medial to the inner ear structures, whereas the contact between it and basioccipital follows the main channel of the CN XII. The metotic foramen is separated from the foramen for the CN XII by a thin lamina of bone. The latter foramen is single and slit-like laterally, but there are two foramina medially that unite along the way out, as shown by the CT scans, being more clearly visible on the left side.

The supraoccipital forms the braincase roof and contributes a small part for the dorsal rim of the foramen magnum (Figure 11C, D). Dorsal to the paroccipital process and medially, close to the dorsal border of the foramen magnum, the supraoccipital shows two small and obliterated foramina. Their identification is still inconclusive, but they could represent either the external foramina connecting to the tympanic sinuses or the exit of a cerebral vein (see below). Similar notches were found in the braincase of *Euparkeria*, but with no such evident connections.

Inner Ear: The semicircular canals are elongate and slender compared to the size of the vestibule, but there is no appreciable difference among them in their lengths or radii of curvature (Figure 13). The anterior semicircular canal leaves the anterior ampulla antero-laterally, runs dorsally and postero-medially to the common crus, going around the auricular fossa. Only the dorsal part of the common crus is surrounded by bone, but since the right side is covered with matrix, it was possible to make a 3D model of that part of the inner ear system. The lateral semicircular canal leaves the anterior ampulla at its postero-lateral portion. It enters the utricular recess at about the same place as the posterior semicircular canal. The posterior semicircular canal has a similar outline to the anterior one when seen in dorsal view. It leaves the posterior ampulla postero-laterally, runs dorsally and antero-medially to meet the anterior semicircular canal. The medial wall of the braincase shows a large internal auditory meatus. By contrast with *Euparkeria*, it is located more anteriorly on the vestibule, so that its posterior-most part is could be reconstructed. The stapes is preserved on the right side (Figure 12C; 13A, B). It is a long rod that tapers distally. The

footplate is in articulation with the fenestra ovalis, but it is very small and does not completely fill the fenestra.

The fenestra ovalis is not particularly big. Both the posterior border of the foramen of the CN VII and the crista interfenestralis are laterally well-developed, so that the fenestra ovalis is somewhat recessed. The dorsal rim of the fenestra ovalis excavates the antero-ventral surface of the paroccipital process while the ventral border extends to the anterior surface of the basal tubera. As the crista interfenestralis is slightly inclined, the fenestra ovalis is located somewhat anterior and dorsal to the metotic foramen. There is no participation of the basioccipital to the postero-ventral rims of the fenestra ovalis. The metotic foramen is big and round, and not sub-divided.

Pneumatic Sinuses: The braincase of *Mesosuchus* possesses a rather well-developed pneumatic system, whose general pattern resembles those found in some theropod dinosaurs (for a detailed description of the pneumatic system, see character 15 of the next chapter). The braincase in general is very trabeculate and possesses many empty cavities. It is thus difficult to follow every ramification of the system, so that confirming the real extension of the sinuses is unlikely. One of the sinus systems is located on the basal tubera. Their main chambers occupy almost the whole of the tubera (Figure 13A, C). They open externally through a pair of foramina close to the lateral borders of the ventral surface of the braincase floor, just posterior to the basal tubera (Figure 12B). In fact, because the suture between basioccipital and basisphenoid is not completely closed, the sinuses can be partly seen in the material in posterior view, filled with matrix (Figure 12B). The sinuses on the basipterygoid processes are also expanded, occupying most of the processes (Figure 13A, C). The foramina connecting the chambers to the outside are more difficult to identify. They do not seem to be confluent with the vidian canals. The main sinuses are connected to other, successively smaller sinues. These, in turn, open dorsally and medially on the basisphenoid, on the braincase floor, just posterior to the hypophyseal fossa – or more anteriorly on the processes, where the medial walls of the bones seem to have been washed away. Also through these ramifications, the basipterygoid sinuses seem to invade the anterior part of the basal tubera, although, as already noted, they do not connect to the sinuses there. The last pneumatic system lies in the paroccipital processes (Figure 13). They are only limitedly expanded in the braincase, not running further distally than half of the total length of the processes. The sinuses enfold the posterior part of the lateral semicircular canals dorsally, ventrally, and laterally (Figure 13C). The left sinus seems to reach a bit further dorsally than the right one. Like the other ones, the foramina that connect the tympanic sinuses to other inner ear structures or to the outside are difficult to identify, but they seem to be connected to the obliterated foramen on the posterior surface of the supraoccipital.

EOHYOSAURUS WOLVAARDTI

Mesosuchus browni and *Howesia browni* are considered key taxa for understanding the origin and early evolution of rhynchosaurs, as many aspects of their anatomy are intermediate between other early archosauromorphs and more derived rhynchosaurs. The material SAM-PK-K10159 was found as loose float on boulder-strewn slopes at the base of a cliff in the *Cynognathus* Assemblage Zone and has been recognised as belonging to a new genus of basal rhynchosaur. The description of the new material is in its final stages of preparation (Butler, Ezcurra, Montefeltro, Samathi & Sobral *in prep*) and the braincase data will be incorporated in a study on the evolution of early rhynchosaur braincases. The material was scanned with an exposure time of 1000ms, 85kV, 400µA, and a voxel size of 22.79µm.

Braincase: The braincase of *Howesia* is disarticulated and not well-preserved internally. However, in general it is very similar to the braincase of *Mesosuchus*. The basioccipital is unfortunately missing. The para- and basisphenoid are present, but since it is not possible to identify the suture between both elements, it will be treated and a single parabasisphenoid. The parabasisphenoid is a much extended element (Figure 14C). In dorsal view, the main core of the bone has an X-shaped form, the anterior two extensions much smaller than the posterior ones. The posterior extensions formed, or contributed to, the basal tubera. The whole of the posterior border of the bone is well delimited, so that the suture with the basioccipital might have been more clearly visible in *Howesia* than in *Mesosuchus* – and was perhaps not interdigitating. The posterioly projecting parts of the parabasisphenoid do not project much ventrally, but it seems clear that the ventral surface of the braincase floor was also depressed in *Howesia*. It is reasonable to assume that the basal tubera were posteriorly projected, as in *Mesosuchus*, just not as pronounced. The basipterygoid processes, on the other hand, are very well marked (Figure 14A, C). They project slightly anteriorly, as well as ventrally. They are oval in cross-section, the longest surfaces directed antero-medially towards each other. They possess pneumatic sinuses (see below). The lateral borders of the hypophyseal fossa seem to be very low, almost non- existent, like in *Mesosuchus*. Likewise, the dorsum sellae is not very tall, but no median depression seems to be present. In *Howesia*, the bottom of the fossa seems to have two deep, rounded depressions. These are definitely not the vidian canals because the vidian canals are positioned more posteriorly. Furthermore, when they reach the fossa, the divisions have disappeared. In fact, these seem to be spaces within the bone. The vidian canals do not meet within the parabasisphenoid. They enter the braincase on the posterior side of the basipterygoid processes, close to the midline, and run parallel until they reach the hypophyseal fossa. The cultriform process is very long and slightly V-shaped, with a shallow groove running along it.

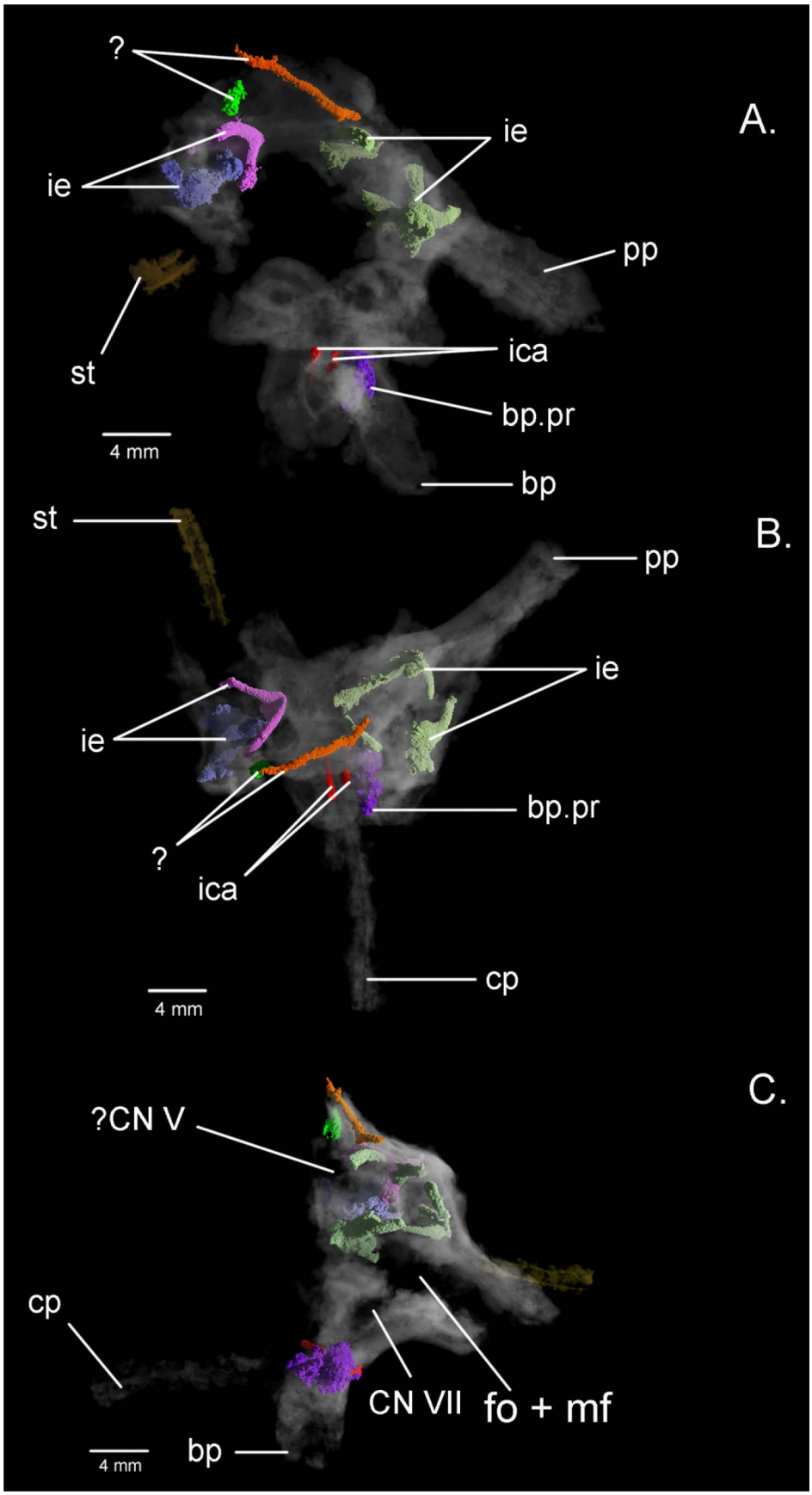

Figure 14: CT scans of the braincase and inner ear of *Eohyosaurus* SAM-PK-K10159 in A) anterior; B) dorsal; and C) left lateral views. bp: basipterygoid process; bp.pr: pneumatic recess of the basipetrygoid process;

The right prootic is disarticulated from all other braincase elements (Figure 14A, B). It is damaged and only the anterior part containing the anterior part of the vestibule / anterior ampulla and the lateral / anterior semicircular canal is present. The left one is also broken and disarticulated, but is more complete than the other. The anterior border of the prootic is notched for the passage of the CN V. The notch is not very deep, and its ventral border is more posteriorly positioned than its dorsal one. The medial wall of the right prootic apparently does not bear such a strongly marked depression for the auricular fossa as does the prootic of *Mesosuchus*. The deeper region which seems to enter the bone is also present, and it is located at about the point where the vestibule is inflated and slightly anterior to the internal auditory meatus, posterior to the anterior ampulla. Because the prootics are damaged, and their articulations with the braincase floor are not well-preserved, identification of the CN VII is problematic on both sides.

The exoccipital and the opisthotic are greatly missing on the right side, although the distal part of the stapes is present. The stapes seems hollow inside. On the left side, the opisthotic is more complete. Its dorsal part is preserved, with the paroccipital process, but the middle ear region is still mostly absent. The paroccipital process is, like in *Mesosuchus*, strongly posteriorly and dorsally directed in relation to the braincase floor, and also flattened antero-posteriorly. The supraoccipital is complete. It houses the postero-medial part of the anterior semicircular canal, the antero-medial part of the posterior semicircular canal and the common crus. This latter was almost completely enclosed by bone, if not entirely. Its exposure on the braincase roof is also strongly antero-dorsally inclined.

Inner Ear: The inner ear of *Howesia* is preserved within the prootic, opisthotic and supraoccipital, but the left side is more complete (Figure 14A–C). The elements on the left side are disarticulated and there is almost no distinction between the main part of the vestibule and the region of the anterior ampulla. The latter extends farther anteriorly, and the lateral semicircular canal enters it postero-laterally. Although the anterior semicircular canal is entirely absent, a slightly bulged region probably marks its medio-dorsal exit from the anterior ampulla. The lateral semicircular canal is not particularly elongate and its radius of curvature is also not pronounced, entering the posterior ampulla abruptly. The posterior semicircular canal leaves this region laterally very close to the LSC, describing a low arch in dorsal view, not extending much anteriorly, into the common crus. The main part of the right vestibule is preserved, but it does not add much to the description.

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cp: cultriform process; CN V: foramen of the trigeminal nerve; CN VII: foramen of the facial nerve; fo: fenestra ovalis; ica: internal carotid artery; ie: inner ear; mf: metotic foramen; pp: paroccipital process; st: stapes; ?: unknown elements.

Pneumatic Sinuses: The braincase of *Howesia* as a whole is also very lightly built and possesses pneumatic sinuses which, in comparison with *Mesosuchus*, are less developed (Figure 14A–C). The basipterygoid processes have a well-marked wall that is proximally thicker and occupied by well-developed and slightly trabeculate spaces. The quality of the scans is not very good and the images are very pixelate, but when compared to the basal tubera, it seems reasonable to infer that these spaces are filled mostly with matrix instead of with porous bone, so that these spaces represent a pneumatic sinus. The basal tubera on the other hand, are mostly bony inside, although they contain well-developed chambers in them. Potential exit foramina for the sinues of the basipterygoid processes were not found. There is also no pneumatic system around the inner ear or in the paroccipital processes.

EUPARKERIA CAPENSIS

Since its discovery and first description by Broom (1913) the small, Middle Triassic archosauriform *Euparkeria* has held a central role in studies of archosaur morphology, phylogeny and biogeography (Sookias & Butler 2013). It was regarded as the sister-group of Archosauria, but recent phylogenetic analyses have excluded phytosaurs from the crown-group and placed it as the immediate sister group of the avialan-crocodilian clade. Also re-examination of “Euparkeriidae” suggests the group may not be monophyletic, and that *Euparkeria* may not lie immediately outside a Phytosauria + Archosauria clade (Sookias et al. 2014). More recently, *Euparkeria* was central to the debate on the origin of avialans – with a special focus given to its braincase (Gower & Weber 1998, Welman 1995). In the occasion, the braincase of UMZC T692 was thoroughly described by Gower & Weber (1998), although the best preserved, isolated specimen, SAM-PK-7696, was not considered in the study. This material was originally described as belonging to *Browniella africana*, but subsequent work by Haughton (1922) has made this a junior synonym of *Euparkeria capensis*. The material was acid prepared and superficially described by Cruickshank (1970), and since then considered in a number of comparative works, but with often divergent anatomical interpretations (eg. Gow 1975, Evans 1986, Walker 1990).

For the first time, the internal anatomy of the braincase and inner ear structures are here accessed. The following description is intended to update knowledge of this particular specimen and to serve as the basis for a discussion on early archosauromorph braincase evolution with a special focus on the middle and inner ears of diapsids more basal than *Euparkeria* – a slightly different treatment as that given by Gower & Weber (1998) and Walker (1990). The material was scanned with an exposure time of 1000ms, 80kV, 250µA, and a voxel size of 16.34µm.

BRAINCASE

The anatomy of the braincase of *Euparkeria* was minutely described by Gower & Weber (1998), and my analysis of SAM-PK-7696 largely agrees with them. However, in the light of a better preserved material and the application of CT techniques, new information could be added to the work of Gower & Weber (1998).

The basioccipital of SAM-PK-7696 is lacking the occipital condyle (Figure 15C–F). The posterior portion of the basioccpital forms an angle of about 135° with its anterior-most tip. The suture between basioccipital and exoccipital was identified in the CT scans as running ventral to the foramen of the CN XII (Figure 17D–F). It shows that the contribution of the basioccipital to the foramen magnum although existent is very limited, not accounting for more than the mid-third of its ventral border. Thus, the depiction of Cruickshank (1970) is slightly exaggerated (Figure 18A). The basioccipital also forms the floor of the metotic foramen. The suture between basioccipital and basisphenoid is straight and runs completely transversely across the braincase, close to the postero-ventral corner of the fenestra ovalis. Thus the basioccipital contributes to the posterior portion of the floor of the fenestra ovalis. Most of the basal tubera are broken-off. The ventral surface of the basioccipital also bears the posterior half of a concavity, as in UMZC T692, and its significance shall be discussed below.

Most of the ventral extension of the parabasisphenoid is missing (Figure 15; 16), including the basipetrygoid processes. It participates on the antero-ventral rim of the fenestra ovalis, but the extension envisioned by Cruickshank (1970) is exaggerated. The suture between parabasisphenoid and prootic was found running antero-posteriorly straight just ventral to the foramen of the CN VII. In his figure 2 (Figure 18B), the bone has a very large ascending process contributing to the anterior border of the fenestra, almost reaching its dorsal rim. The suture indicated by him is likely a preservation artifact that caused the prootic to fold on the right side over the paths of both the palatine and hyomandibular branches of the CN VII, ventral and dorsal to its foramen, respectively. On the left side, there is less distortion. The straight nature of the suture between parabasisphenoid and prootic is also in contrast with the description given by Ewer (1965:391) where the parabasisphenoid has “two [dorsally] expanded wings, separated by an incurved concave area”. The depictions of Gower & Weber (1998) are more congruent with the arrangement found here. Furthermore, the suture with the basioccipital also contradicts Cruickshank’s (1970:684) interpretation of the parabasisphenoid as having a “small posteriormost process in front of the ventral ramus of the opisthotic”. According to his figure 2, this would mean the parabasisphenoid extended posteriorly on the floor of the fenestra ovalis, which is not the case.

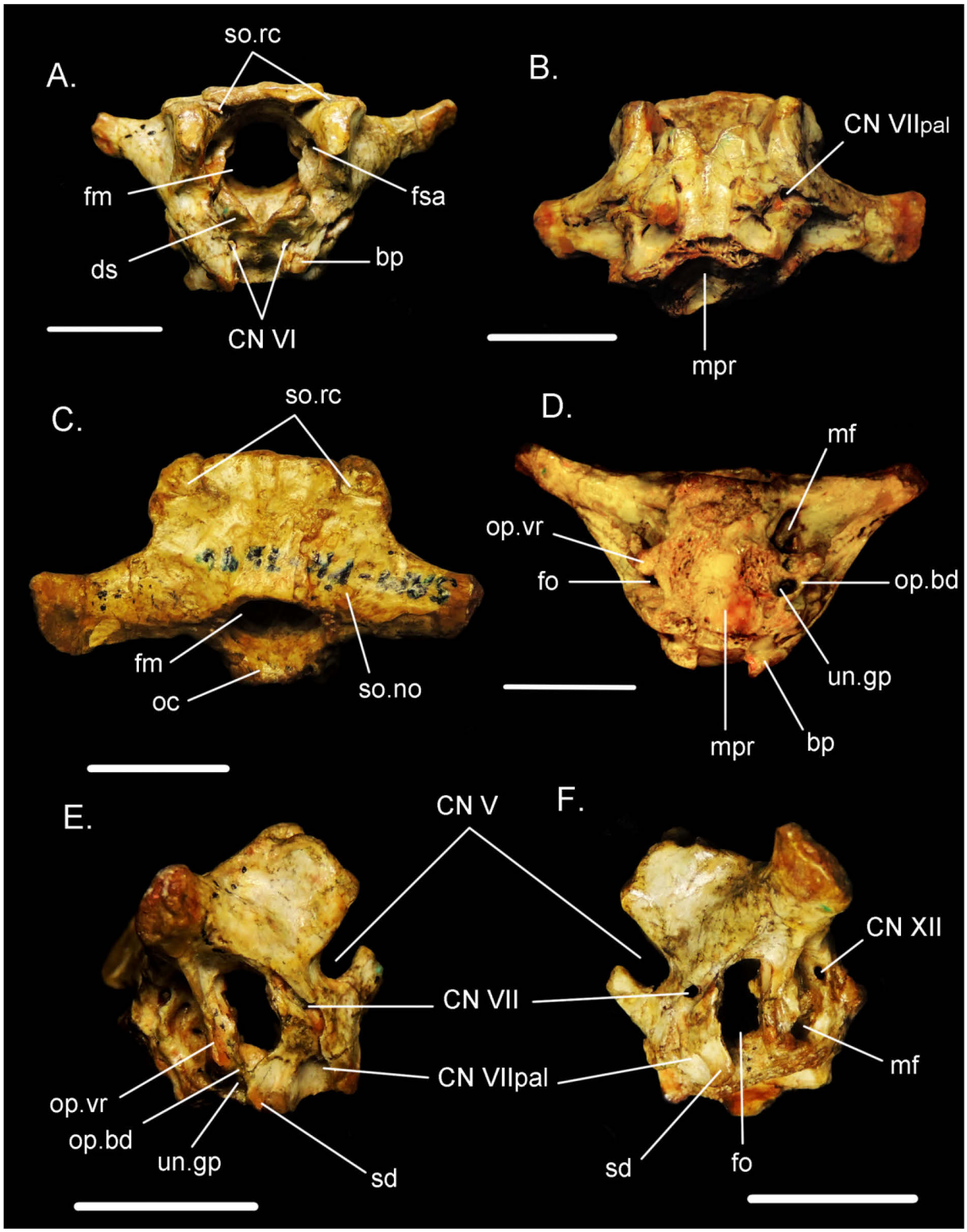

Figure 15: Braincase of *Euparkeria capensis* SAM-PK-7696. A) anterior view; B) Antero-ventral view; C) Dorsal view; D) Ventral view; E) Right lateral view; F) Left lateral view. bp: basipterygoid process; CN VI: foramen of the abducens nerve; CN V: foramen of the trigeminal nerve; CN VII: foramen of the facial nerve; CN VII_{pal}: course of the palatine ramus of CN VII; CN XII: foramen of the hypoglossal nerve; ds: dorsum sella; fm: foramen magnum; fo: fenestra ovalis; fsa: fossa subarcuata; mf: metotic foramen; mpr: medial pharyngeal recess; oc: occipital condyle; op.bd: opisthotic bridge; op.vr: ventral ramus of the opisthotic; so.no: supraoccipital notch; sd: semilunar depression; so.rc: supraoccipital recess; un.gp: unnossified gap. Scale bars equal 1 cm.

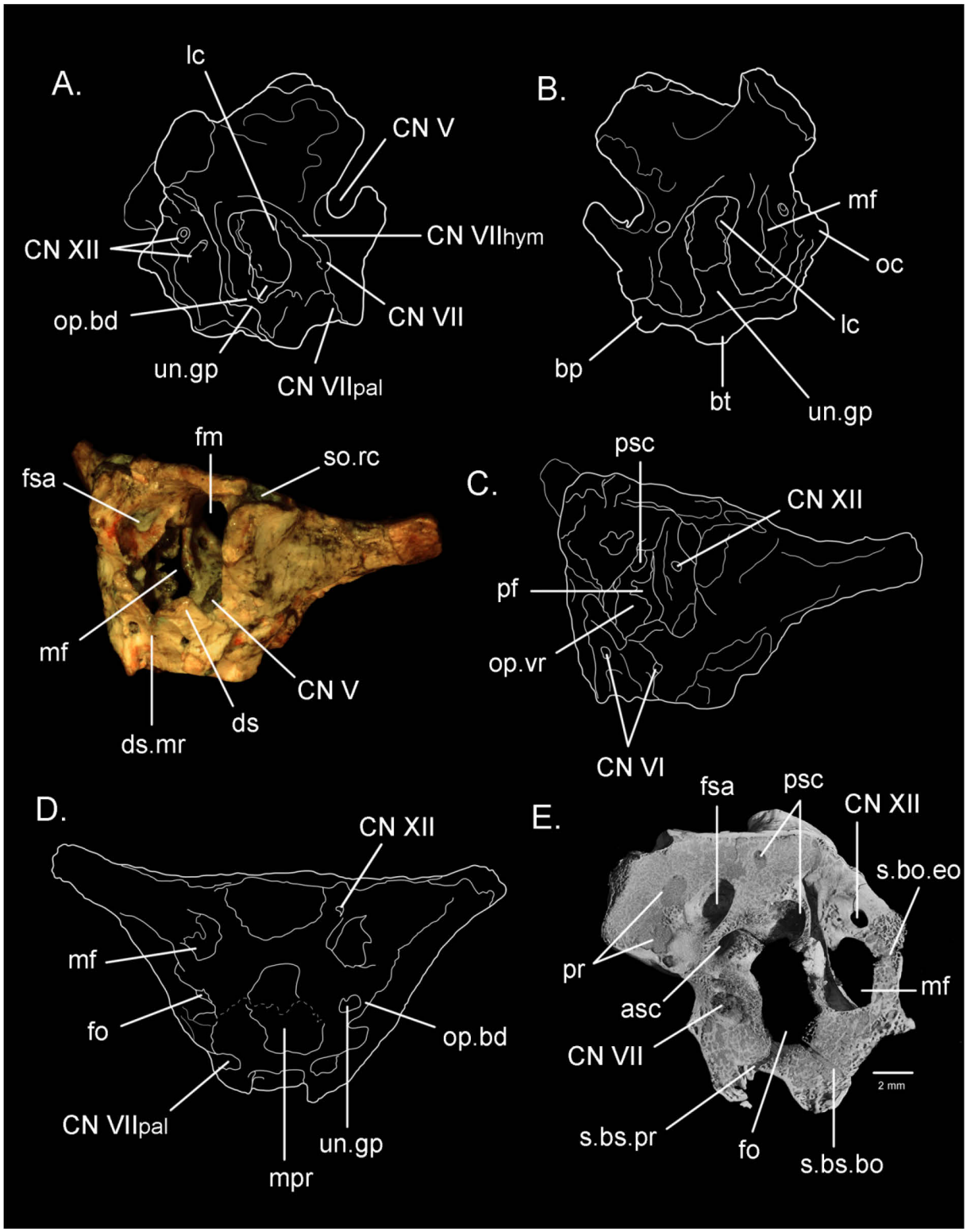

Figure 16: Braincase of Euparkeria. A) Drawing of right lateral view; B) Drawing of left lateral view; C) Braincase in antero-lateral view; D) Drawing of ventral view; E) CT image of right medial wall. asc: anterior semicircular canal; bp: basipterygoid process; bt: basal tuber; CN V: foramen of the trigeminal nerve; CN VI: foramen of the abducens nerve; CN VII: foramen of the facial nerve; CN VIIhym: path of the hyomandibular branch pf CN VII; CN VIIpal: path of the palatine branch of the CN VII; CN XII: foramen of the hypoglossal nerve; ds: dorsum sella; ds.mr: dorsum sella medial ridge; fm: foramen magnum; fo: fenestra ovalis; fsa: fossa subarcuata;

On the posterior portion of the right lateral surface of the parabasisphenoid, antero-ventrally to the fenestra ovalis, there is a small fold of bone, forming a sulcus (Figure 15E, F). It is positioned postero-ventrally to the foramen of the CN VII and a similar structure was identified by Gower & Weber (1998) as the “semilunar depression”. There seems to be a similar structure on the right side, although less well-marked (see below). Anterior to the semilunar depression, the lateral surface of the parabasisphenoid is deeply concave. On the anterior region of this concavity ran the palatine branch of the facial nerve, probably extending ventrally on the posterior surface of the basipterygoid process, as is the usual topographical relationship of these structures (Oelrich 1956, Sobral *et al*. 2012). The ventral surface of the parabasisphenoid bears the anterior portion of the marked fossa that extends posteriorly onto the basioccipital (Figure 16D).

The posterior third of the braincase floor is flat. It then slopes ventrally, and a low median ridge can be seen running antero-posterioly in the middle, dividing it into left and right halves (Figure 16A). Its anterior third flattens again and the ridge disappears. However, on both sides of the floor, two big, oval depressions are found with their longer axis slightly directed postero-lateral to antero-medial. The anterior parts of these depressions seem to be a bit deeper than the posterior ones. They are separated by a rather thick portion of the braincase floor.

The supraoccipital is wide and has a very flat dorsal surface. It participates quite extensively on the dorsal border of the foramen magnum, as shown by Cruickshank (1970 – Figure 18A). It is restricted to the skull roof, not extending much ventrally, but partially housed the common crus, the posterior portion of the anterior semicircular canal and the anterior part of the posterior semicircular canal. The suture line between opisthotic and exoccipital bends dorsally at its postero-medial portion (see below), what could indicate the posterior extension of the supraoccipital is more extensive than that shown by Cruickshank (1970). The contact between supraoccipital, prootic and opisthotic (Figure 17D–F) runs dorsally from the anterior surface of the base of the paroccipital process, from the dorsal rim of the fenestra ovalis, and then anteriorly along the dorsal part of the prootic. The anterior-most limit between them is, however, harder to identify. Together with the prootics, the supraoccipital probably takes part in the antero-lateral notches for the articulation with the posterior wings of the parietals (Ewer 1965). No epiotic was found.

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lc: lagenar crest; mf: metotic foramen; mpr: medial pharyngeal recess; oc: occipital condyle; op.bd: opisthotic bridge; op.vr: ventral ramus of opisthotic; pf: perilymphatic foramen; pr: pneumatic recess; psc: posterior semicircular canal; s.bo.eo: suture between basioccpital and exoccipital; s.bs.bo: suture between basisphenoid and basioccipital; s.bs.pr: suture between basisphenoid and prootic; so.rc: supraoccipital recess; un.gp: unnossified gap.

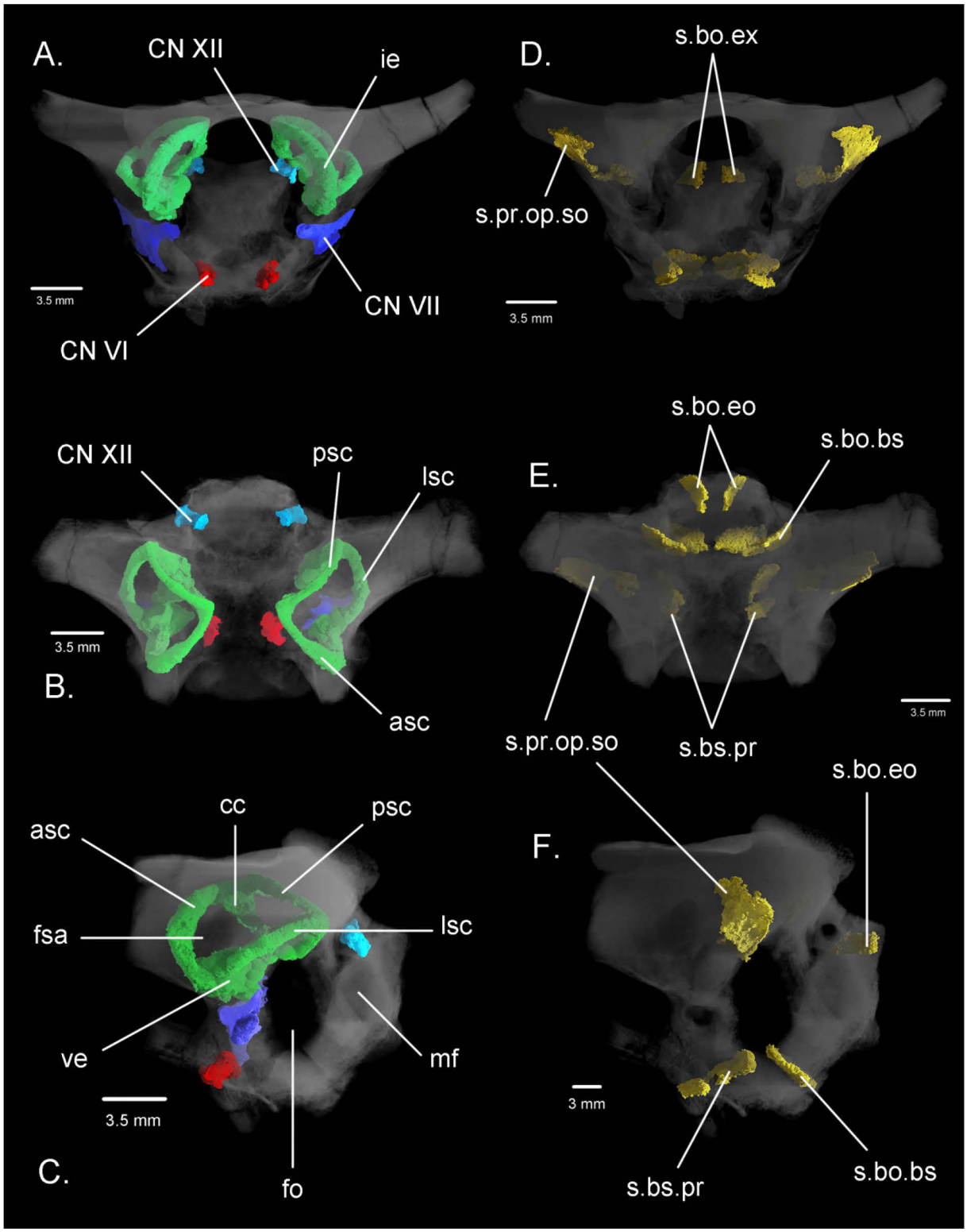

Figure 17: CT images of the braincase of Euparkeria. A–C) Inner ear structures in anterior, dorsal and left lateral views, respectively; D–F) Sutures between bones in anterior, dorsal and left lateral views, respectively. asc: anterior semicircular canal; cc: cmmon crus; CN VI: foramen of the abducens nerve; CN VII: foramen of the facial nerve; CN XII: foramen of the hypoglossal nerve; fo: fenestra ovalis; fsa: fossa subarcuata; ie: inner ear; lsc: lateral semicircular canal; mf: metotic foramen; psc: posterior semicircular canal; s.bo.eo: suture between basiccopital and exoccipital; s.bo.bs: suture between basioccipital and basisphenoid; s.bs.pr: suture

As already mentioned, the exoccipital participated not only on the lateral rim of the foramen magnum, but also on the lateral thirds of its ventral border. The contact between exoccipital and basioccipital does not extend much anteriorly and thus the exoccipital contributes only to the posterior wall of the metotic foramen (Figure 17D). Also, a suture line was found on the dorsal limit of the exoccipital indicating its contact with the opisthotic – confirming the assumption of Gower & Weber (1998) that the exoccipital is restricted to the pillar between the foramen magnum and the metotic foramen. The contact between exoccipital and supraoccipital likely lies close to the suture with the opisthotic (see below), but since the medial extension of the suture was not definitely found, the actual participation of the exoccipital on the dorso-lateral margins of the foramen magnum cannot be determined. On its lateral surface, there are two foramina for the anterior and posterior branches of the CN XII – the posterior one is slightly bigger and more dorsally located.

The opisthotic forms the majority of the paroccipital processes, and the triple suture between it, supraoccipital and prootic indicates that there is a little participation of the latter on the anterior base of the process (Figure 17D–F). The ventral ramus of the opisthotic runs ventrally from the base of the paroccipital process and bends slightly posteriorly on the right side, and more sharply on the left. It separates the fenestra ovalis anteriorly from the metotic foramen posteriorly and therefore is also referred to as crista interfenestralis. The processes protrude latero-posteriorly as well as dorso-distally. They are dorso-ventrally flattened and twisted so that the ventral surface is slightly anteriorly directed. The distal tips are slightly rounded and separated from the main body of the processes by a delicate neck. The distal-most tip of the right side is missing. The processes are excavated ventrally by the dorsal borders of both the metotic foramen and the fenestra ovalis (recessus stapedialis), and the crista interfenestralis sends a ridge dorsally along and until the mid-point of its ventral surface. On the posterior base of the paroccipital process two notches excavate the braincase, close to the lateral rim of the foramen magnum. Their interpretation is unclear, but they certainly do not represent the exit foramina of the vena capitis dorsalis, as the CT scans show no traces of internal paths (Figure 15C). Contrary to Cruickshank (1970), the opisthotic does not participate in the borders of the foramen magnum. On the ventral border of the right fenestra ovalis, there is a sagittal bony contact between the ventral ramus of the opisthotic and the posterior region of the parabasisphenoid. This bony contact forms the lateral limit of a small aperture whose medial part is delimited by the lateral surface of the parabasisphenoid forming the braincase floor. On the left side, the bony bar is broken-off.

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between basisphenoid and prootic; s.pr.op.so: suture between prootic, opisthotic, and supraoccipital; ve: vestibule.

The area ventral to this region was identified by Cruickshank (1970) as the lagenar recess (Figure 18), whereas Gower & Weber (1998) identify it as an “unossified gap”. This structure will be discussed below.

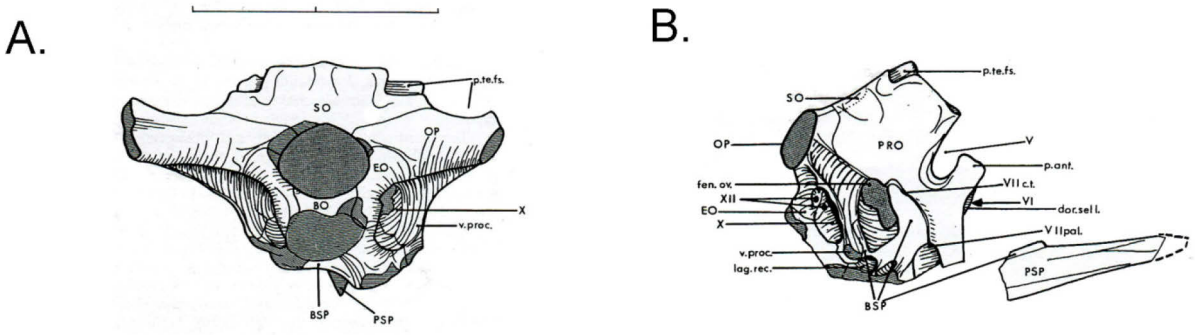

Figure 18: Braincase of Euparkeria SAM-PK-7696 as interpreted by Cruickshank (1970). Scale bar equal 2 cm. BO: basioccipital; BSP: basisphenoid; c.t.: chorda tymapni branch of the CN VII; dor.sel.: dorsum sellae; EO: exoccipital; fen.ov.: fenestra ovalis; lag.rec.: lagenar recess; OP: opisthotic; p.ant.: pila antotica; p.te.fs.: poste-temporal fenestra; pal.: palatine branch of the CN VII; PRO: prootic; PSP: parasphenoid; SO: supraoccipital; v.proc.: ventral process. Roman numerals refer to corresponding cranial nerves. From Cruickshank (1970).

The anterior region of the braincase was either unossified or not preserved. If the former, it would correspond to the condition seen in other basal archosauriforms, but there seems to be indications of the presence of a laterosphenoid in other specimens of *Euparkeria* (eg. Gower & Weber 1998, Clark *et al*. 1993). Therefore, the prootic is the anterior-most element of the lateral braincase wall of this specimen. Postero-ventral to the foramen of the CN V, the prootic is slightly depressed, indicating the position of a gasserian ganglion external to the brain cavity (Figure 15E, F; 16A, B). Connecting the base of the paroccipital process with the depressed area for the external ganglion, the prootic shows a low faint ridge, a short crista prootica, indicating the position of the lateral semicircular canal (Figure 15E, F; 16A, B; 17C). The crista parotica descends anterior to the single opening of the CN VII, projecting slightly posteriorly and forming a fold of bone that almost conceals its anterior border. A narrow but very deep groove can be seen running postero-dorsally from the dorsal border of the foramen of the CN VII to the antero-dorsal rim of the fenestra ovalis, indicating the path of the hyomandibular branch (Figure 16A). A similar groove for the palatine branch is found running from the ventral border of the foramen, connecting to a very big and depressed area on the lateral surface of the parabasisphenoid.

The medial wall of the prootic possesses a big, round and very deeply marked fossa immediately dorsal and slightly posterior to the foramen for the CN V, indicating the position of the fossa subarcuata (auricular fossa – Figure 16C, E; 17C). The posterior wall of the fossa has a marked, deeper sub-region that seems to enter the bone but it does not lead

anywhere within the bone, as shown by the CT scans. Its identification is thus unknown. Ventral to the fossa subarcuata, the left foramen of the CN VII is separated from the inner ear by an elevated and rounded ridge – whose lateral part, close to its base, seems to bear a dorso-ventral sulcus, perhaps leading to the foramen of the CN VII or to the ventral part of the brain cavity. The foramen of the CN VII is connected to the oval depressions on the anterior third of the braincase floor by a groove. The prootics meet anteriorly in the midline, forming the dorsum sellae. The dorsal borders of the sellae are M-shaped with a central, low ridge running dorso-ventrally, lateral to which there can be found the foramina for the CN VI. The lateral surfaces of the dorsum sellae are slightly protruded medially, forming a rim and faintly concealing the lateral border of the foramina.

INNER EAR

The inner ear is (Figure 17A–C) very well preserved and compared to the overall size of the braincase, it is much enlarged. The semicircular canals are not especially elongate when compared to the preserved dorsal part of the vestibule, and none of them seem particularly longer than the other two. The postero-ventral part of the vestibular area is not enclosed by bone, as laterally the rim of the fenestra ovalis is much dorsally extended and as medially the internal auditory meatus is largely unossified. The anterior semicircular canal exits the anterior ampulla from its anterior and slightly lateral area, running immediately dorsally and posteriorly, and then medially, around the fossa subarcuata, entering the common crus antero-dorsally. Only the dorsal-most part of the common crus is surrounded by bone, but its ventral connection with the utriculus is marked on the medial wall of the braincase, so that its course can be reconstructed. The anterior and posterior semicircular canals meet at about the mid-length of the vestibule, but the crus communis enters the utriculus just anteriorly to the dorsal rim of the fenestra ovalis, extending ventrally and posteriorly. The posterior semicircular canal leaves the posterior portion of the utricular recess dorso-laterally and runs antero-medially into the common crus. In dorsal view, it describes a rather concave arch, while the path of the anterior semicircular canal is slightly convex. The lateral semicircular canal is slightly shorter than the others. It leaves the postero-lateral portion of the anterior ampulla, describing a gentle arc in dorsal view, and enters the recessus utriculi also laterally.

The fenestra ovalis is large and oval. It is formed mostly by the prootic anteriorly and the opisthotic posteriorly, but there is participation of the basioccipital postero-ventrally and of the parabasisphenoid ventrally (Figure 17F). On the anterior and posterior walls of the fenestra ovalis, at about its mid-height, the lagenar crests can be found. They mark the dorsal-most limit of the lagenar recess and separate the vestibular and cochlear regions of the inner ear (Figure 16A, B). The anterior crest is low and round, while the posterior one is

taller and thin. On the left side, the posterior crest is complete, but on the right side its main body is broken off, and only the dorsal and ventral parts of the base remain. The ventral-most tip of the lagenar recess lies in the unossified, medial to the bony bar connecting the ventral ramus of the opisthotic and the postero-dorsal region of the parabasisphenoid, and lateral to the braincase floor (Figure 15E, F; 16A, B). The right crista interfenestralis extends medially in a curious manner, forming a vertical W with prolonged dorsal and ventral ends (Figure 16C). The dorsal fold of bone bears the posterior part of the utricular recess, where the ventral part of the posterior and the posterior part of the lateral semicircular canals conjoin. The middle edentate part could have bordered the perilymphatic duct laterally. On the left side, this medial projection is less well-marked.

The metotic foramen is also much enlarged. Laterally the width is fairly the same, but medially it is wider ventrally than dorsally. On the posterior wall of the foramen, there are two foramina. The posterior-most is the biggest. Anterior and slightly ventral to it, there is another foramen which is somewhat smaller. These represent the anterior and posterior branches of the CN XII. On the left side, the area is slightly damaged, so that only one of the branches of CN XII is visible, presumably its posterior ramus. The CN X exited the braincase through the metotic foramen, together with the glossopharyngeal and accessory nerves and the vena cephalica posterior (in case it did not leave via the foramen magnum). The metotic foramen had an irregular shape medially, and this could indicate the position of the strutures housed by the foramen or exiting through it. The ventral portion is wide and round, and likely represents the area where the perilymphatic sac bulged and sat. The foramen connecting this recessus scalae tympani area to the cochlear recess is not complete, but the medial projection of the crista interfenesralis seems to have bordered the perilymphatic tube laterally in its mid-height, as already described. The perilymphatic sac might have been big, as the recessus scalae tympani area represents more than half of the foramen. The nerves and the vein would have left the brain cavity dorsally to the perilympahtic sac, where medially the metotic foramen is narrower.

As already noted, the foramen of the CN VII is small, slightly bigger than the posterior branch of the CN XII, and on the right side it is mostly concealed by a fold of bone probably representing a deformed crista parotica. On the left side, distortion is absent, but still the foramen sits in a recess, formed by the crista anteriorly, a small crest posteriorly and by the routes of the hyomandibular and palatine branches, dorsally and ventrally respectively. The hyomandibular branch of the facial nerve leaves the braincase on the postero-dorsal part of the foramen towards the base of the paroccipital process, whereas the palatine branch exits ventrally, bordering the posterior surface of the basipterygoid process. The foramen of the trigeminal nerve is the biggest of all cranial nerves. It is formed by the prootic and is incomplete on its antero-dorsal border. Laterally, the posterior region of the foramen is

slightly depressed, indicating the external position of the gasserian ganglion in relation to the brain cavity. The ventral and antero-ventral borders are formed by the ossification of part of the base of the embryonic pila antotica, which is usually referred to as the inferior anterior process of the prootic. The abducens nerve foramina are located on the dorsum sellae, laterally at about their mid-heights. The lateral borders of the foramina are partially hidden by the elevated lateral surfaces of the dorsum sellae. These elevated parts represent the ossification of the other part of the bases of the pilae antotica.

DISCUSSION

A number of features were discussed thoroughly by Gower & Weber (1998) on the braincase of *Euparkeria*. Many of these are connected to Welman's (1995) phylogenetic hypothesis between Euparkeria and avialans and, consequently, to his identifications concerning the metotic foramen and the fenestra pseudorotunda and need not be further discussed here. Some other features, however, can be confirmed or corrected in the light of new information yielded by the CT scans and by advances in braincase studies in the past 15 years.

Facial Foramen: Two separate foramina for the palatine and hyomandibular branches of the facial nerve were identified first by Ewer (1965), and followed by Cruickshank (1970) and to a lesser extent by Evans (1986). Only one opening for the CN VII was found in SAM-PK-7696. As correctly noted by Gower & Weber (1998), the area identified as housing the palatine foramen in the former papers is but a deeply depressed area on the lateral surface of the parabasisphenoid, and there is no foramen located here. As mentioned above, the crista parotica of the prootic seems to have been distorted, and folded backwards as to conceal the sulci of the branches, and it might give the impression a ventrally directed foramen existed. Since different foramina for the hyomandibular and palatine branches of the facial nerve was one of the characters surveyed here and not found in any taxa until more derived theropods and avialans, it is safe to state that such a separation did not occur until much later in archosaurian evolutionary history and that there is no such individual variation in *Euparkeria* as suggested by Gower & Weber (1998).

Unossified Gap: The area between the distal tip of the ventral ramus of the opisthotic and the posterior portion of the parabasisphenoid was identified by Cruickshank (1970) as the lagenar recess and by Welman (1995) as the fenestra pseudorotunda. Gower & Weber (1998) elegantly corrected Welman's (1995) interpretations and identified it as an unossified gap instead. Although neither the prootic nor the basioccipital seem to take part in it, the homologisation of this structure with other unossified gaps in the same region of a number of

diapsids seems accurate. In this specimen of *Euparkeria*, the gap is very similar to that of *Sphenodon* where it is dorsally confluent with the otic capsule (Säve-Söderbergh 1947). Here it is identified as forming the distal-most part of the lagenar recess, since the relationship of these structures with each other seems consistent throughout a number of diapsid taxa (Gower & Weber 1998, Oelrich 1956). The bony connection between opisthotic and parabasisphenoid is present on the right side forming the ventral rim of the fenestra ovalis, as indicated by Cruickshank (1970) and not identified in Gower & Weber (1998). It therefore resembles stem group archosaurs surveyed by Gower & Sennikov (1996). Due to the preservation state of UMZC T692, it seems likely that this connection was damaged. On the left side, the bony bar is missing, and the more marked posterior direction of the ventral ramus of the opisthotic gives the unossified gap a larger size.

Semilunar Depression: Immediately anterior to the unossified gap there is a shallow depression on the lateral surface of the parabasisphenoid. The postero-dorsal border of this depression is open and confluent with the unossified gap ventral to the fenestra ovalis. The antero-ventral border is delimited by a crest of bone of the parabasisphenoid on the proximal end of the basal tuber. The term was introduced by Evans (1986:186) for *Prolacerta* and subsequently identified in other archosauriforms. Of the putative functions given for this structure, the articulation with the ventral ramus of the opisthotic seems rather unlikely. Evans (1986, fig. 7) illustrates the ventral ramus as antero-ventrally directed towards the crest, delimiting the depression anteriorly. However, in the actual specimen, the ventral ramus is slightly bent at its mid-portion, so that the distal-most part is clearly ventrally directed.

Pneumatisation: No true pneumatic cavity was found in the sense of an internal space within a bone connected through a foramen to other external spaces such as the middle ear cavity or the pharyngeal sinus. However, CT scanning revealed trabeculate, rather than compact, bone histology. To the pneumatic system often belong shallow recesses that does not necessarily perforate adjacent bones, and to these can be included here the ventral fossa on the braincase floor and the lateral depression of the parabasisphenoid. The first may be part of the basisphenoid recess (medial pharyngeal recess of Gower 2002), whereas the latter may be related to the basipterygoid recess or the anterior tympanic recess (*sensu* Witmer & Ridgley 2009). No true anterior tympanic recess (ATR) could be identified, nor the trabeculate cavity of Welman (1995). However, depressions on similar topographic areas of the parabasisphenoid have been identified in a number of taxa as the ATR, as for example in *Shuvosaurus* (Chatterjee 1993), *Postosuchus* (Gower 2002), and *Lewisuchus* (Bittencourt *et al*. 2014), and could possibly represent homologous structures – although a proper

investigation was not carried out here and needs to be considered carefully. We confirm that the eustachian tubes were not enclosed by bone.

Others: The position of the perilymphatic foramen identified here agrees with the assumption of Gower & Weber (1998) that a notch on the medial surface of the ventral ramus of the opisthotic represents the lateral half of an incompletely ossified foramen. The dorsal extension of the parabasisphenoid is another problematic feature of *Euparkeria*. The suture between prootic and parabasisphenoid was identified in the CT scans as running straight postero-dorsally to antero-ventrally just ventral to the facial and trigeminal foramina, antero-ventrally to the fenestra ovalis. With this conformation, the identification of Ewer (1965) and Cruickshank (1970) seems incorrect, and more similar to that of Gower & Weber (1998). The lateral depression is, however, formed entirely by the parabasisphenoid. It is currently not possible to know if in other specimens of *Euparkeria* the conformation would be the same, and if this truly represents individual variation.

DYSALOTOSAURUS LETTOWVORBECKI

The small bipedal ornithopod *Dysalotosaurus lettowvorbecki* Virchow, 1919, was recovered during the well-known German Tendaguru Expeditions between 1909 and 1913. The Middle Dinosaur Member, from which *Dysalotosaurus* was collected, is dated as Late Jurassic (late Kimmeridgian; Witzmann *et al*. 2008). Much of the recovered material, which consisted mostly of disarticulated bones, but also included more complete specimens, was unfortunately destroyed during the Second World War and was never studied in detail (Janensch 1955, Maier 2003). The name *Dysalotosaurus* was first published in 1919, and the material started to be formally described by Pompeckj (1920), who died during the course of this work. Subsequently, *Dysalotosaurus* was carefully studied by Janensch (1955), whose work was based on material that includes the braincases used in the present study, as well as drawings and photographs of the by then already lost specimens. The genus *Dysalotosaurus* has been regarded as a junior synonym of the North American genus *Dryosaurus* (e.g., Galton 1977, 1983) and both genera were placed in their own clade within “Hypsilophodontidae”. Dryosauridae was only formally proposed years later (Milner & Norman 1984). Although this synonymy was accepted by many subsequent authors (e.g. Forster 1990, Coria & Salgado 1996, Weishampel *et al*. 2003, Norman 2004), more comprehensive phylogenetic studies recovered *Dryosaurus*/*Dysalotosaurus* as a basal iguanodontian, following the earlier proposals of Janensch (1955) and Pompeckj (1920). Recently, this synonymy has been contested (Hübner & Rauhut 2010, McDonald *et al*. 2010,

Barrett *et al*. 2011). As noted by Hübner (2011), Galton (1977, 1983) based his conclusions on similarities between both of the dryosaurid genera that, according to his own work (Galton 1974), were less significant than the degree of intraspecific variation within the genus *Hypsilophodon*. Many anatomical differences exist between the two genera in the skull and postcranial skeleton, especially in the pelvis and hind limbs (Barrett *et al*. 2011, Hübner 2011). Therefore, in the present study, *Dysalotosaurus* will be treated as a separate genus.

BONES OF THE BRAINCASE, SKULL ROOF AND SKULL FLOOR

Basioccipital: The three elements of the braincase floor are tightly sutured (Figure 19). The basioccipital predominantly forms the occipital condyle, except for minor lateral contributions from the exoccipitals (Janensch 1955). As in other ornithopods (Galton 1974), the basioccipital is hemispherical and has a smooth articular surface. In posterior view, it has a flat surface around the inferior border of the foramen magnum and is thicker ventrally than laterally. Ventrally, the basioccipital is concave and possesses a round and wide ridge with a slight central recess that extends medially. In lateral view, it forms a neck from which protrudes the occipital condyle. The condyle is marked by porosities near its base (Figure 19B). The posterior portion of the sutural area for the opisthotic is almost straight, but the bone then curves gently ventrally at an angle of approximately 11°, giving the dorsal rim of the basioccipital a slightly convex shape in lateral view. Such curvature is also reported for Tenontosaurus (Winkler *et al*. 1997). In ventral view, the surfaces around the basal tubera form a channel-like structure that indicates the position of the suture between the basioccipital and the basisphenoid, as shown by the CT scans (Figure 19B). The sutural area for the basisphenoid has a concave outline laterally, where the basal tubera fit, and a convex outline ventrally. At the ventral contact with the basisphenoid, the basioccipital surface steeply rises from the neck of the condyle and forms a thin triradiate structure, with one ridge extending medially and the other two laterally, but not perpendicularly to each other, in the direction of the base of the tubera. The area between the meeting point of the three ridges posteriorly and the apex formed by the limits of the basioccipital-basisphenoid suture anteriorly forms a shallow fossa.

Basisphenoid and Parasphenoid: The basisphenoid forms the anterior part of the braincase floor (Figure 19). The basal tubera are well developed, and in ventral view they have round posterior margins and tapering anterior ones, which extend to meet the bases of the basipterygoid processes. The basipterygoid processes project very strongly

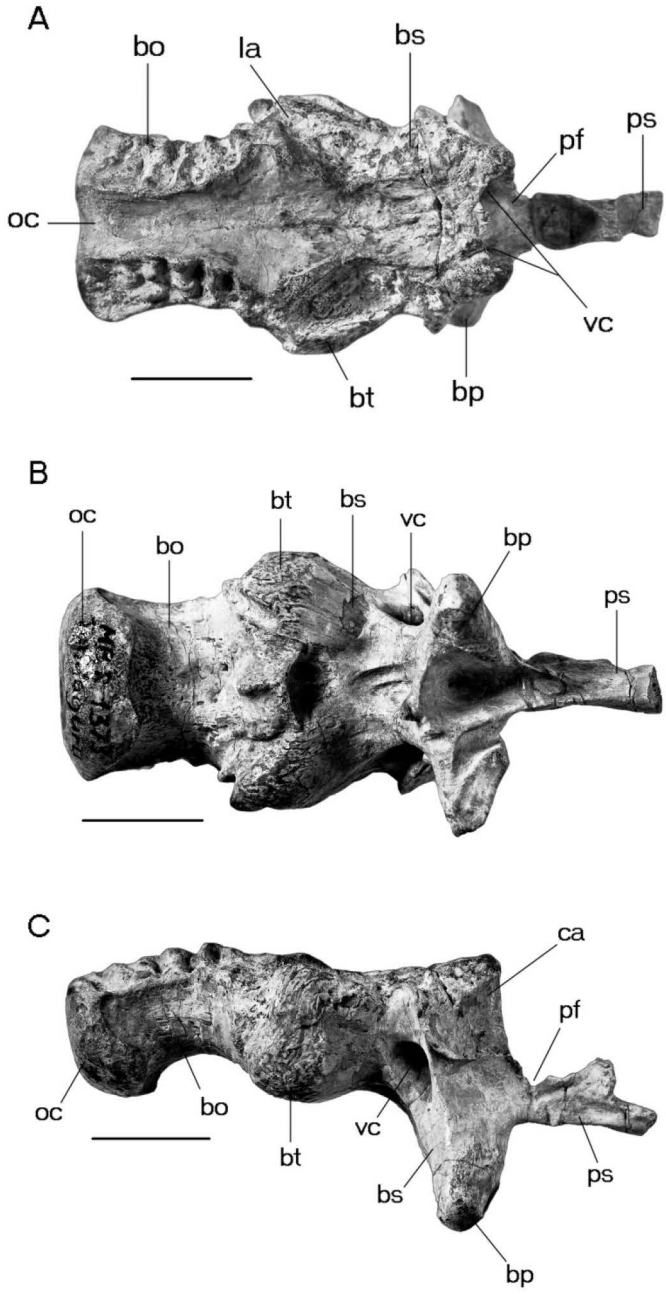

Figure 19: Skull floor bones (MB.R.1373) of *Dysalotosaurus*. A) Dorsal view; B) Ventral view; C) Right lateral view. bo, basioccipital; bp, basipterygoid process; bs, basioccipital; bt, basal tuber; ca, crista alaris; la, lagenar recess; oc, occipital condyle; vc, vidian canal; pf, pineal fossa; ps, parasphenoid. Scale bars equal 1 cm.

ventrolaterally in anterior view, with their rounded, pronounced tips pointing slightly posteriorly in lateral view. In ventral view, a recess is formed posteriorly between the bases of the basipterygoid processes (Figure 19B). The anterior surface of this recess rises sharply together between the basipterygoid processes, forming a wall between them. The anterior surface of this wall constitutes the posterior margin of a very deep pit that lies between the basipterygoid processes, which was erroneously described by Janensch (1955) as the

pituitary fossa. This pit indicates the position of a closed embryonic structure, the hypophyseal fenestra (Balanoff *et al*. 2010), and is also found in *Hypsilophodon* (Galton 1974). In lateral view, a sharp ridge along the margin of each basipterygoid process separates it into anterior and posterior surfaces. The posterior surface bears a very large and well-defined foramen for the entrance of the cerebral branch of the carotid artery and the palatine branch of the facial nerve (CN VII). The anterior border of the foramen is formed by the ridge, which at this point curves slightly posteriorly and partially hides the foramen in lateral view (Figure 19C). Above the foramen, the canal for the palatine branch of CN VII is short but well defined. In anterolateral view, the anterior surface of the basipterygoid process has three different and well-delimited areas, one above the other. The upper part is a flattened area with a strongly rounded outline. This is part of the crista alaris and the place of attachment of the superior part of the M. protactor pterygoideus (Oelrich 1956, Galton 1974, 1989, Weishampel & Bjork 1989). The inferiormost area lies at the tip of the basipterygoid process. It is also flat and shows muscle attachment marks just above the articular surface for the pterygoid, which probably indicates the point of origin of the inferior part of the M. protactor pterygoideus (Oelrich 1956). Between these two regions, the basisphenoid is smooth and gently concave and very likely indicates the path of a vein. The pattern is very similar to that found in the iguanid lizard *Ctenosaura*, but Oelrich (1956) mentions it simply as the 'internal jugular vein'. In an attempt to solve much of the confusion involving the terms 'jugular vein' and 'internal jugular vein', we give a more extensive and deeper discussion on vein nomenclature in the next section. Here, we propose that this vein is better identified as the vena capitis lateralis, based on the descriptions of Bruner (1908) and the descriptions and nomenclature of Großer and Brezina (1895), Dendy (1909), and O'Donoghue (1920).

The clearly visible Vidian canals are not obstructed by sediment and extend anteromedially to the pituitary fossa, on the anterodorsal part of the basisphenoid. The pituitary fossa of *Dysalotosaurus* lacks the sella turcica, as well as a dorsum sellae and the foramina for the abducens nerve (CN VI). Galton (1989:pl. 1, fig. 8 – Figure 20) noted the presence of these foramina, but we regard this determination as problematic because the CT images show no sign of a channel inside the bone that would define the route of this nerve through the basisphenoid. Furthermore, there are no indications of external openings for this nerve on the posterodorsal surface of the pituitary fossa. CN VI may have been housed in a very shallow canal on the anterior surface of the braincase floor and left the braincase anteriorly, without piercing the bone. Galton (1989:pl.1, figure 8) also labels a sella turcica, but we do not agree with this identification. Because the basisphenoid is not damaged, it could be that the anterior region of the braincase was cartilaginous in life, resembling the

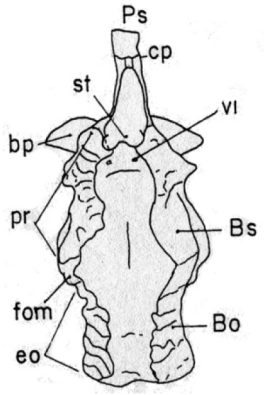

Figure 20: Dorsal view of the braincase floor of *Dysalotosaurus* as interpreted by Galton (1989). Bo: basioccpital; bp: basipterygoid process; Bs: basisphenoid; cp: cultriform process; eo: exoccipital; fom: fenestra ovalis plus metotic foramen; pr: prootic; Ps: parasphenoid; st: sella turcica; VI: abducens nerve.

condition in the lizard *Ctenosaura*, even if it is confirmed that this specimen was not fully grown (Hübner 2011). In dorsal view, the braincase floor is narrow posteriorly, and widens considerably at the area of the basal tubera, almost reaching the external lateral limit of the bone. It then constricts again to broaden slightly near the front of the basisphenoid. Although the suture between the basi- and parasphenoid cannot be identified in the CT images, the bone clearly has a higher density anterior to the anterior border of the pituitary fossa. For this reason, we decided to describe the rostrum as being formed by the parasphenoid. The cultriform process is gently convex and bears a smooth groove on its dorsal surface. In both MB.R.1373 and MB.R.1367, the anterior-most limit of the rostrum cannot be determined due to lack of preservation.

L a t e r o s p h e n o i d : The laterosphenoid contacts the parietal along most of its dorsal surface and has a small contact with the supraoccipital on its posterodorsal border (Figure 21). It has no contact with the basisphenoid, being excluded by an oblique contact with the prootic. The bone is a four-sided element that roughly resembles a trapezium in outline, because its anterior margin is distinctly shorter than the posterior one. It has a steeply inclined ventral margin, which makes it dorsally directed. Like the laterosphenoids of *Hypsilophodon* (Galton 1974) and *Zephyrosaurus* (Sues 1980), it is anteroposteriorly concave and dorsoventrally convex, so that it has a smooth crest extending transversally on its lateral surface. The anterodorsal part of the laterosphenoid projects laterally, with a rounded end that contacts the frontal and the postorbital, fitting into a cavity formed by both of the latter bones, as seen in Hypsilophodon and other basal ornithopods (Galton 1974, Sues1980, Norman *et al*. 2004). On its posteroventral corner, close to the prootic, the laterosphenoid possesses two short but well-marked channels with high bordering ridges.

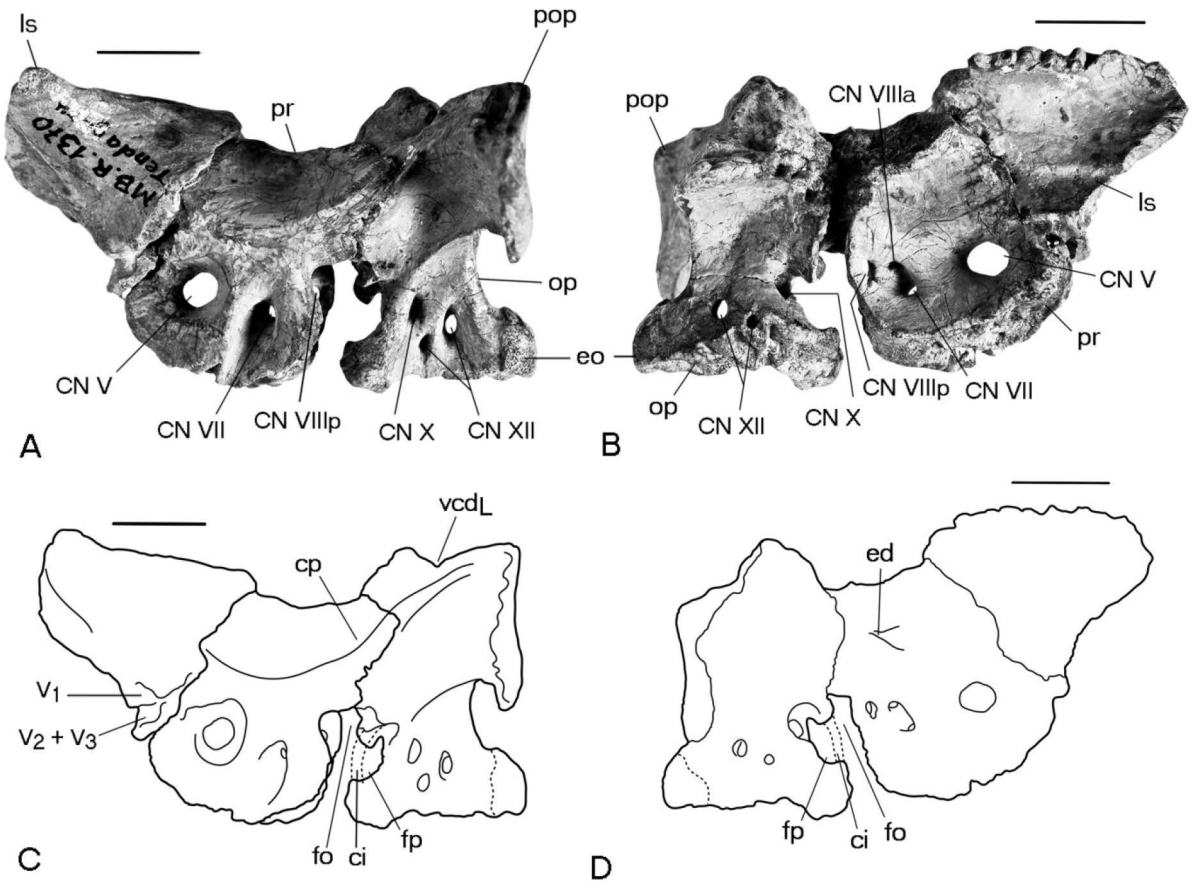

Figure 21: Braincase wall (MB.R.1370) of *Dysalotosaurus*. A) Photo in right lateral view; B) Photo in medial views, C – D) Schematic drawings of the same. ci: crista interfenestralis; CN: cranial nerves (a, anterior ramus; p, posterior ramus); cp: crista prootica; ed: endolymphatic duct; eo: exoccipital; ls: laterosphenoid; op: opisthotic; fo: fenestra ovalis; fp: fenestra pseudorotunda; pr: prootic; pop: paroccipital process; pr: prootic; V,: branches of trigeminal nerve (1, ophthalmic nerve; 2, maxillary nerve; 3, mandibular nerve); vcdL: vena capitis dorsalis lateral branch. Scale bars equal 1 cm.

The channels diverge to extend anterodorsally and anteroventrally. The former channel might have carried the ophthalmic division of the trigeminal nerve (V_1), whereas the latter, which is deeper and slightly wider, may have transmitted the maxillary and the mandibular divisions of the nerve (V_2 and V_3, respectively). Both channels lead to the anterior margin of the very large foramen for the trigeminal nerve (CN V) situated on the anterior margin of the prootic. In medial view, the laterosphenoid is triangular in outline and concave, with its dorsal margin more strongly arched to form part of the skull roof. It is subtly divided into two dorsoventrally concave areas, an anterior and a posterior one. In the area where the laterosphenoid, prootic, parietal, and supraoccipital converge, the bones do not contact each other, but enclose a foramen. The presence of this opening is not due to poor preservation, as confirmed by the CT scan and discussed in depth in the next section, and we identify it as the foramen for the passage of the vena capitis dorsalis.

Parietal: The fused parietals form a complex element that roofs the braincase anterodorsally (Figure 22). In dorsal view, the parietals have four strongly protruding wings that give it an 'X'-shaped outline. In lateral view, each parietal is strongly twisted outwards from its midpoint, so that the dorsally facing surfaces of the anterior wings become laterally directed on the posterior wings. The dorsal rim of the posterior wings is very high and convex. The anterior wings have round sockets at their lateral borders for their contacts with the postorbitals (Norman *et al*. 2004), and a ridge extends from the anterior rim of the sockets to the point where the parietal begins to twist. Dorsal to the ridge, the parietal surface is flat, but ventrally the surface is excavated, especially close to the end of the ridge.

This ridge was the point of insertion of the M. pseudotemporalis superficialis and M. adductor externus medius (Oelrich 1956, Galton 1989). Because of the presence of ventral projections of the supraoccipital (see below), the parietals only contact the laterosphenoids and are excluded from contact with the prootics and opisthotics. In dorsal view, between the anterior wings, the parietals possess a short median notch for the articulation of the frontals. Another small notch protrudes between the twisted posterior wings of the parietals. This notch forms the anterior-most end of a ridge, which is continued by medial nuchal crest of the supraoccipital (Figure 22A). The posterior part of the ventral surface of the parietal extends steeply dorsally as to form a deep pit that bears two foramina at its bottom (Figure 22B; see below).

Supraoccipital: The supraoccipital is tightly fused to the parietals, but the suture line between both elements could be traced in the CT images. It roofs the posterior and posterolateral regions of the brain cavity (Figure 22) and has a small participation in the dorsal margin of the foramen magnum, consisting only of a shallow notch. This conformation is similar to that found in Thescelosaurus (Galton 1997), but contrasts with the condition in other basal ornithopods, where the supraoccipital contributes to much of the dorsal rim of the foramen magnum (Galton 1974, Norman *et al*. 2004). It confirms a general trend among basal iguanodontians to reduce the contribution of supraoccipital to the margin of the foramen magnum; in more derived forms, the supraoccipital is completely excluded from the border of this foramen (Weishampel & Bjork 1989, Norman 2004).

In ventral view, the surface of the supraoccipital is smooth, having almost no suture lines between it and the parietals. Close to its external borders, the supraoccipital forms large ventral projections at the lateral margins, which contact the opisthotic and prootic and have a short contact with the laterosphenoid more anteriorly (Figure 22B, C). Only small portions of these projections are visible in lateral view (Figure 22C). The triangular contact surface for the prootic and the subrectangular surface for the opisthotic bear the traces of inner ear

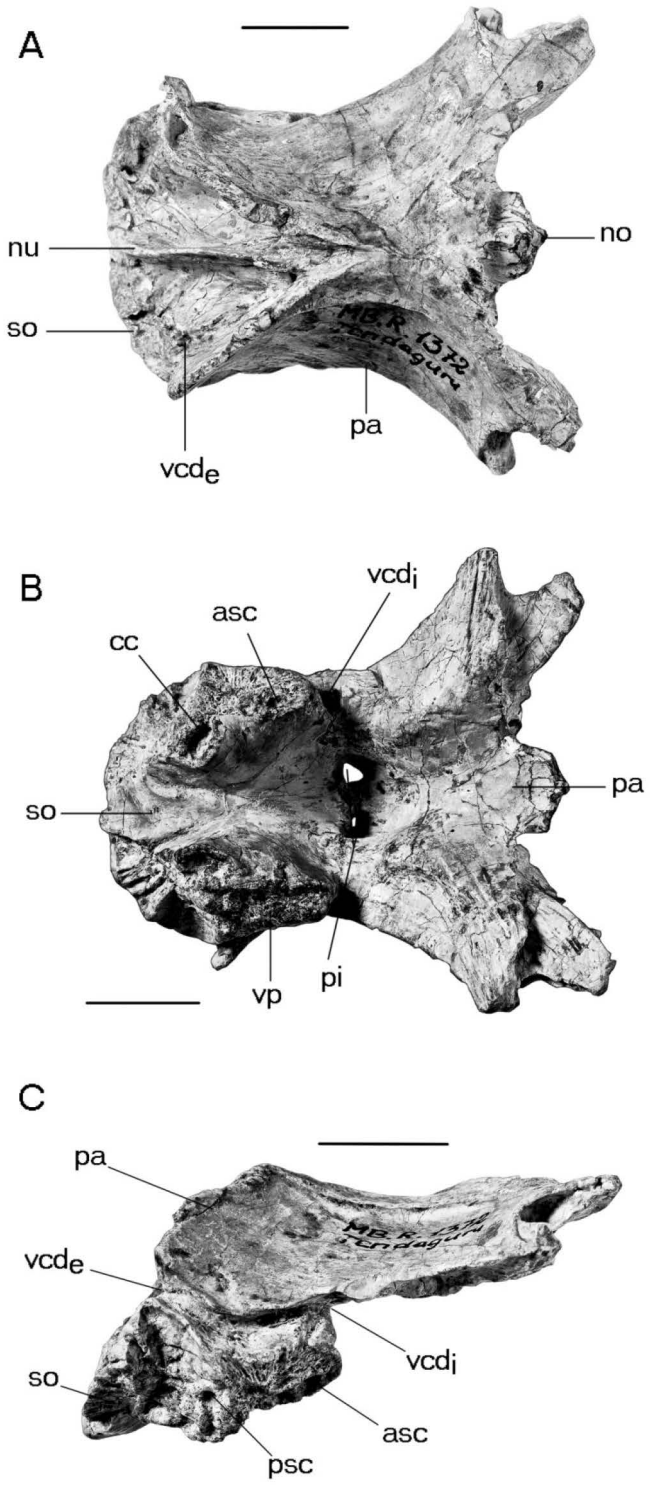

Figure 22: Skull roof (MB.R.1372) of *Dysalotosaurus*. A) Dorsal view; B) Ventral view; C) Right lateral view. asc: anterior semicircular canal; cc: common crus; no: notch; nu: nuchal crest; pa: parietal; pi: pineal foramen; psc: posterior semicircular canal; so: supraoccipital; vcd: vena capitis dorsalis (e, external foramen; i, internal foramen); vp: ventral projection. Scale bars equal 1 cm.

structures, especially on the right side. On the contact surface with the prootic, the cross section of the anterior semicircular canal can be seen anteriorly and the cross-section of the posterior semicircular canal is found on the contact surface with the opisthotic. A large and deep recess can be found on the medial corner between these two sutural surfaces and represents the junction between these canals, the common crus (Figure 22B; 23C, D). Dorsally, the nuchal crest runs anteroposteriorly from the posterior notch of the parietals to the posterior-most margin of the supraoccipitals. The dorsal surfaces of the supraoccipitals are rough and wedge-shaped and they are bordered laterally by the high rims of the posterior wings of the parietals. Each of the surfaces lateral to the nuchal crest narrows anteriorly, at the end of which two foramina are found, separated by the nuchal crest. Due to high rims of the posterior wings of the parietals, they are only visible in posterodorsal view. These foramina were termed 'post-parietal gaps' by Janensch (1955). The anterior part of the ventral surface of the supraoccipital also runs steeply dorsally, forming the posterior border of a deep ventral pit. This pit lies exactly at the midpoint of the braincase and was probably associated with the longitudinal sinus and pineal gland (Sampson & Witmer 2007). Thus, the 'post-parietal gaps' can be regarded as the parietal foramina.

Directly behind the dorsal openings of the parietal foramen, the supraoccipital bears two deep fossae. These fossae are not present in *Hypsilophodon* or *Thescelosaurus* (Galton 1974, 1997), iguanodontians (Weishampel & Bjork 1989, Norman 2004), or other basal ornithopods (Norman *et al*. 2004). Janensch (1955) described them as a small parietal foramen, noting that Pompeckj (1920) had compared them to the foramen present in Varanus. However, Pompeckj (1920) did not recognize the structures of *Dysalotosaurus* as homologous to the structures of *Varanus*, because in other *Dysalotosaurus* materials he observed not only one, but many small fossae. CT scanning thematerial did not reveal any internal channels associated with these fossae. If they represent foramina, then these were obliterated well before the full ossification of the supraoccipital. CT scans revealed a channel within the supraoccipital/parietal suture on either side of the skull that is distinct from the rest of the sutural line (Figure 24). Both its external and internal apertures are so subtle that they are barely visible and were mentioned neither by Janensch (1955) nor Galton (1989). The channel opens dorsally close to the external border of the surface between the parietal and the supraoccipital, and then extends diagonally between the bones. Ventrally, it opens just anterior to the ventral projection of the supraoccipital, in the area of the foramen formed by the parietal, supraoccipital, laterosphenoid, and prootic. This channel represents the route of the main trunk of the vena capitis dorsalis, which will be further discussed below.

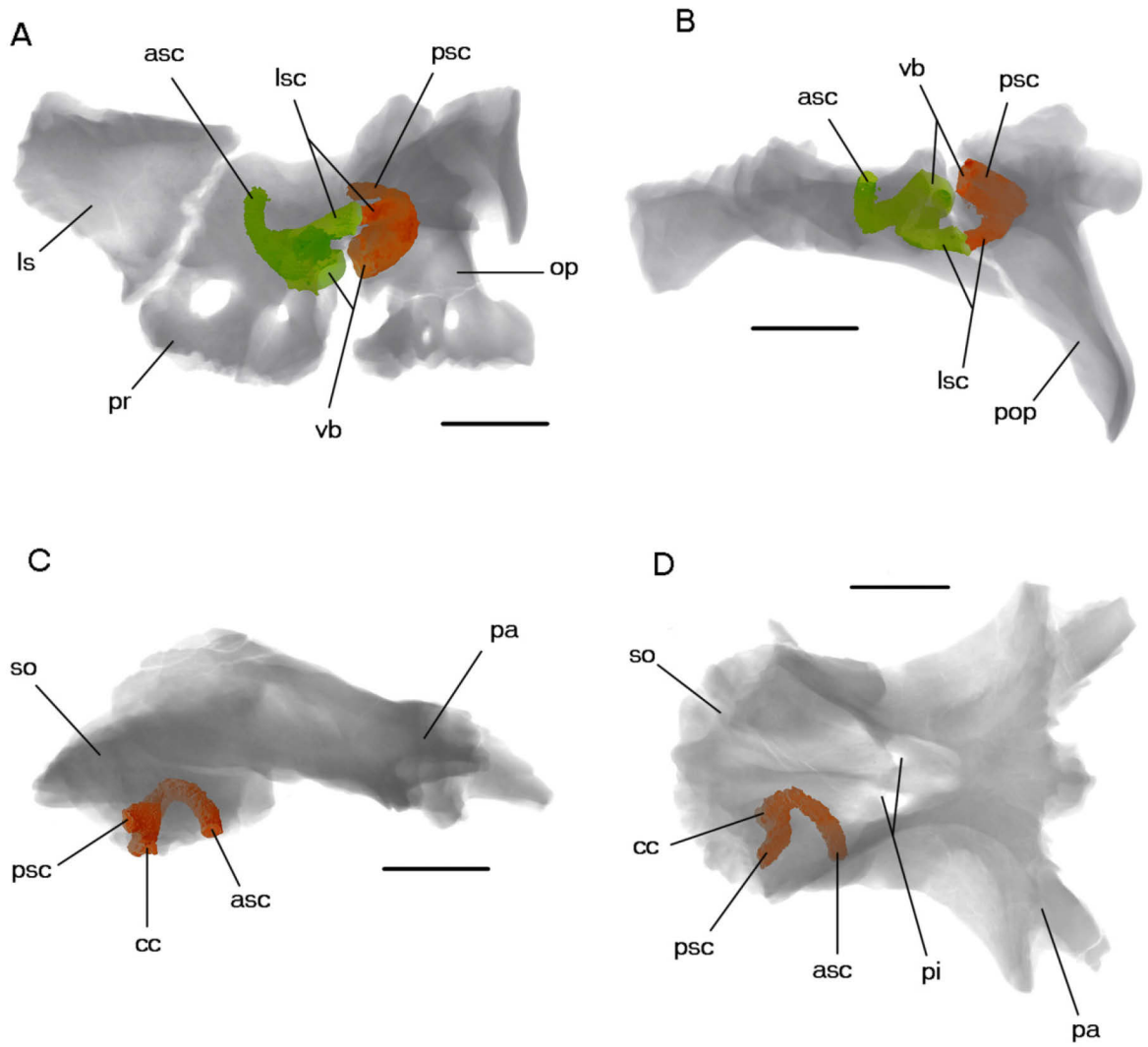

Figure 23: Inner ear of *Dysalotosaurus* visualized by computed tomographic images. A) Lateral and B) Dorsal view of braincase wall; C) Right lateral and D) dorsal view and of the skull roof. Asc: anterior semicircular canal; cc: common crus; ls: laterosphenoid; lsc: lateral semicircular canal; op: opisthotic; pa: parietal; pi: pineal foramen; pop: paroccipital process; pr: prootic; psc: posterior semicircular canal; so: supraoccipital; vb: vestibule. Scale bars equal 1 cm.

E x o c c i p i t a l : The exoccipital is fused to the opisthotic and can be identified in MB.R.1367 as a tetrahedral structure (Figure 21). The bone is located at the posterior-most portion of the opisthotic and forms the ventrolateral border of the foramen magnum (at the level of the cranioatlantal joint) and the upper lateral part of the occipital condyle. It has no contact with the supraoccipital or parietal and does not contribute to the paroccipital process or to the otic capsule.

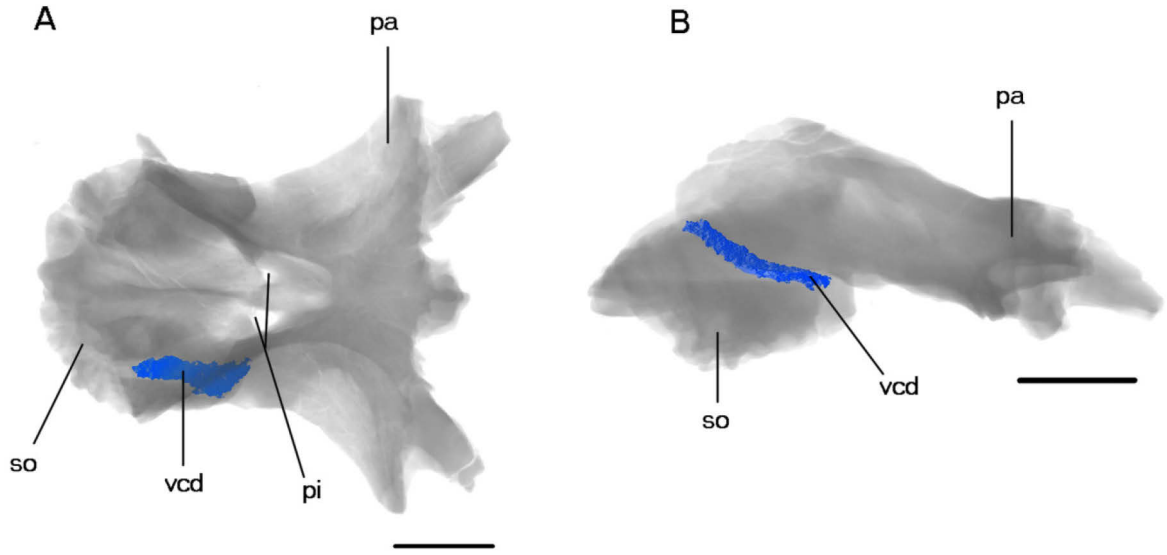

Figure 24: Vena capitis dorsalis of *Dysalotosaurus* as seen by CT images inside the skull roof. A) Dorsal and B) Right lateral views. Pa: parietal; pi: pineal foramen; so: supraoccipital; vcd: vena capitis dorsalis. Scale bars equal 1 cm.

Prootic: The prootic forms the mid-lateral wall of the braincase and contacts the laterosphenoid, basisphenoid, opisthotic, and supraoccipital, but has no contact with the parietal (Figure 21). In lateral view, the upper surface of the prootic is concave, and continuous with that of the laterosphenoid, and its dorsal margin is anteroposteriorly shorter than its ventral one. It tapers posteriorly towards its articulation with the opisthotic, its posterior tip overlapping the latter element. Thus, the prootic forms part of the base of the anterior facet of the paroccipital process. A rounded ridge separates the dorsolateral surface of the prootic from its ventral part. Posteriorly, this ridge turns into the sharp crista prootica (attachment site of the M. levator pterygoideus; Norman 2004), just dorsal to the fenestra ovalis close to the point where it contacts the opisthotic. The ventral part of the lateral surface of the prootic is flat and pierced by two foramina located side by side and separated by a thin ridge. The anterior opening is very large and bears no sign of subdivision and represents the foramen for the trigeminal nerve (CN V) and the middle cerebral vein, with no participation from the laterosphenoid in its margin. The posterior foramen is smaller and marks the exit for the facial nerve (CN VII). Directly dorsal to the trigeminal foramen, on the anterior area of the longitudinal rounded ridge (crista alaris), muscle attachment markings indicate one of the sites of origin for the M. pseudotemporalis superficialis (Oelrich 1956). Ventral to the trigeminal foramen there is another muscle attachment site, whose overall posterior outline is continued on the alar process of the basisphenoid, and which served as the point of origin of the superior part of the M. protactor pterygoideus (Oelrich 1956, Galton

1974, 1989, Gower 2002). The foramen for the facial nerve lies deep in a recess and its ventral border forms a channel that is continued on the surface of the basisphenoid dorsally and leads to the opening of the Vidian canal. This channel carried the palatine branch of CN VII. The route of the hyomandibular branch is less pronounced, but a shallow depression can be seen on the dorsal border of the foramen, leading slightly posteriorly. The prootic forms the anterior border of the fenestra ovalis.

In medial view, the prootic is smooth and slightly concave dorsoventrally. The large trigeminal foramen is clearly visible, but the facial nerve foramen opens into a common fossa (deep acoustic recess). Apart from that for CN VII, two other apertures are visible in the deep acoustic recess: a large one placed posterior to the facial nerve foramen and a very small one placed between and dorsal to both of these openings. The posterior opening indicates the exit of the posterior ramus of the acoustic (or auditory) nerve (CN VIII) and opens into the otic capsule, whereas the dorsal opening is for the anterior ramus of the same nerve. Thus, in contrast to *Hypsilophodon* (Galton 1974), the foramen for CN VIII is rotated and can be seen laterally in posterolateral view. This configuration is similar to the arrangement found in the lizard Ctenosaura (Oelrich 1956). Dorsal to the deep acoustic recess, there is a shallow excavation extending anteroposteriorly and narrowing posteriorly. Janensch (1955) described this as a narrow foramen leaving the labyrinth immediately dorsal to the facial foramen, and connected to the latter by a short groove, but he did not identify this structure. Due to the presence of the excavated area anterior to it, Galton (1989) identified this feature as the fossa subarcuata. Sues (1980) described a similar structure in Zephyrosaurus as the entrance for the 'vena cerebralis media'. However, taking into consideration the morphology of the osseous labyrinth, the structure is probably a part of the channel that housed the endolymphatic duct (Figure 21D), as in *Ctenosaura* (Oelrich 1956). Between the deep acoustic recess and the entrance channel for the endolymphatic duct, the prootic shows a swollen area, the tympanic bulla, which houses the anterior ampullary recess and part of the vestibule (Oelrich 1956). See below for more details on the morphology of the otic capsule.

O p i s t h o t i c : The opisthotic forms the posterior part of the lateral wall of the braincase, and forms much of the lateral and dorsal rims of the foramen magnum. It contacts the prootic, supraoccipital, and basioccipital, and has very small contacts with the basisphenoid and parietal (Figure 21). In lateral view, it is a narrow bone with a prominent and laterally directed paroccipital process. This process is approximately straight but its posterior surface is somewhat concave, especially in the proximal part. The anterior surface is also concave and its midline bears a marked ridge, which is the continuation of the crista prootica. Overall, this continuous crest has a sinuous outline that starts with a smooth crest on the lateral projection of the laterosphenoid, passes onto the prootic (becoming sharper at the crista prootica), and

rounds again on the paroccipital process of the opisthotic, fading out close to the distal end of the process. This ridge divides the anterior surface of the process into two approximately equal halves. The dorsal half is slightly concave and served as the pathway for the occipital artery (Oelrich 1956). The ventral half bears a deep groove, especially proximally, directly dorsal to the fenestra ovalis, forming the stapedial recess. In coronal cross-section, the process flattens slightly and narrows dorsoventrally before expanding again to form the distal-most part of the process, which is rounded. On the dorsal surface of the proximal end of the paroccipital process, a shallow channel extends from the suture with the prootic, passing over the process to the other side, so that in occipital view a semilunate excavation is present. Janensch (1955) mentions this feature as a venous path, but did not specify which. Following the work of Bruner (1908), we consider it to be for the lateral branch of the vena capitis dorsalis.

In lateral view, the opisthotic forms the posterior border of the fenestra ovalis and entirely houses the fenestra pseudorotunda. However, the division between these openings is not preserved because the crista interfenestralis is broken, and both structures form a single opening. At the dorsal border of the otic capsule, the opisthotic bears a notch where the dorsal-most part of the crista interfenestralis would have been situated, and at the ventral border there is a round, smooth bulge indicating the ventral-most end of the crista, indicating the original presence of this feature. The ventral border of the otic capsule was not ossified, because there is no bony contact between the prootic and the opisthotic. The fenestra ovalis is slightly dorsally positioned, and the fenestra pseudorotunda has a slit-like outline. Posteriorly, on the lateral surface of the opisthotic, three foramina are placed side-by-side. The anterior one is slightly dorsally displaced, the medial one is very small and more ventrally positioned, and the posterior one is the largest of the three and very elongate in shape (see below for further discussion). In medial view, the opisthotic has a generally dorsoventrally concave outline and a short surface. Two features are clearly visible: three foramina and a very deep fossa in the center of the surface. Janensch (1955) identified the latter ‘closed pore’ as the entrance to a foramen that became closed during ontogeny and that served as the pathway for the posterior cerebral vein. Galton (1989) agreed with this idea and Sues (1980) identified a similar structure in *Zephyrosaurus*. However, a similar structure is not present in *Hypsilophodon* and Galton (1974) postulated that in this taxon the posterior cerebral vein left the braincase through the metotic foramen. The posterior-most of the three foramina lies very close to the suture with the exoccipital. The anteriormost foramen is somewhat anteromedially positioned and starts at the otic capsule, then extends diagonally, and exits behind the fenestra pseudorotunda on the lateral wall of the opisthotic. Finally, the middle foramen is very small and located near the suture with the basioccipital. The posterior and the middle foramina represent the posterior and anterior branches of CN

XII, respectively, whereas the anterior one is the vagus foramen. The medial wall is partially open forming the internal auditory meatus.

INNER EAR

CT scanning results suggest that the internal structure of the ear of *Dysalotosaurus* (Figure 23) did not differ significantly from the condition in the lizard *Ctenosaura* as described by Oelrich (1956). Comparisons and terms used herein are based on his work and that of Wever (1978), unless stated otherwise. The vestibule forms a large longitudinal cavity in the opisthotic posteriorly and prootic anteriorly, with a total length of 13.84 mm, width of 5.77 mm, and height of 4.11 mm. It can be seen on the medial surfaces of the opisthotic and prootic as an inflated area, termed the auditory bulla. Further anteriorly, and somewhat more dorsally positioned, the anterior ampullar recess is present, which housed the anterior and lateral ampullae. The foramen for the posterior ramus of the auditory nerve (CN VIII) opens into the anterior-most part of the vestibule, whereas the foramen for the anterior ramus of CN VIII opens into the more posterior region of the anterior ampullar recess, where the lateral ampulla was located. The lateral semicircular canal (total length of 11.78 mm) extends at the level of the crista prootica and has a slight anteroposterior inclination: when the posterior portion of the basioccipital is positioned parallel to the horizontal stereotaxic plane, the posterior end of the lateral semicircular canal lies more dorsally than the anterior semicircular canal. The lateral semicircular canal extends from the posterior part of the anterior ampullar recess and then enters the opisthotic, describing a gentle curve in dorsal view and running slightly dorsally in lateral view. In the opisthotic, the lateral semicircular canal meets the posterior semicircular canal in the posterior ampullary recess, where both canals form the posterior sinus. The anterior region of the anterior ampullary recess housed the anterior ampulla, and from it the anterior semicircular canal (11.48 mm in length, 13.37 mm in height) describes a curve dorsally, extending first slightly anteriorly and then strongly posteriorly, exiting the prootic dorsal to the trigeminal foramen and piercing the supraoccipital. The posterior semicircular canal (11.43 mm long and 11.19 mm high) extends dorsomedially and slightly anteriorly, also in a curved manner, exiting the opisthotic on its dorsal surface close to its medial rim and entering the supraoccipital. From this point it extends dorsally and anteriorly very subtly and bends sharply medially, to meet the anterior semicircular canal at the common crus. The common crus is located in a dorsal position within the otic capsule, excavating the supraoccipital only partially, thereby differing slightly from the description of Galton (1989), who stated that it lay solely within the supraoccipital. On the prootic, in coronal view, there is a slender ridge at the level of the dorsal border of the posterior ramus of CN VIII, the lagenar crest, which separates the vestibule from the lagenar recess (as in many other examples, the terminology of this structure, when mentioned, is variable and the

term ‘crista vestibuli’ can also be used; see Gower, 2002:57). This recess housed the perilymphatic cistern laterally and the lagena more medially. The lagenar recess extends into the basioccipital and basisphenoid as in *Zephyrosaurus* (Sues, 1980). The cochlea had an estimated length of 9.67 mm, as measured from the distance between the lagenar crest and the ventral margin of the prootic.

DISCUSSION

On the Identification and Nomenclature of Oto-occipital Veins and their Foramina: The nomenclature of reptilian head vasculature is complex and confused. Janensch (1936) described the general pathways of cephalic veins for saurischians and ornithischians, focusing on the venae cerebralis anterior (not relevant for this study), medial, and posterior, and their osteological correlates. Most of the statements he made concerning these two last veins are in error, but were subsequently used by Galton (1974, 1989) as a basis for identifying various braincase structures.

Galton (1974, 1989) and Janensch (1936), as well as many other recent paleontological descriptive studies, misinterpreted a number of vascular terms, including the ‘vena cerebralis posterior’ and ‘vena jugularis interna’ (sometimes also called the ‘vena jugularis’). Following Dendy (1909), O’Donoghue (1920), and Baumel (1993), the jugular vein is formed by the fusion of all of the veins that drain blood from the head and neck, with its external ramus serving the anterior part of the skull (the draining veins forming the vena cephalica anterior and others) and the internal ramus draining the brain and occipital regions. Thus the vena jugularis interna represents the confluence of veins that include the vena capitis medialis and the vena cephalica posterior. The latter drains blood “mostly from the veins of the brain via the cranial dural sinuses and from the inner ear and suboccipital regions” (Baumel 1993:448).

The vena cephalica posterior originates from the posterior half of the sinus longitudinalis (Figure 25A) and in more derived lepidosauromorphs, it shifts its course from the vagus foramen in the embryo to the foramen magnum in the adult (Bruner 1908). The pattern found in adult *Sphenodon* seems to indicate a plesiomorphic condition, where the posterior cephalic vein leaves the braincase through the lateral braincase wall (O’Donoghue 1920). In the adult crocodilian, “the blood vessels exit the foramen magnum, or both the exits mentioned above [foramen magnum and ‘metotic fissure’] for the posterior cerebral vein are used” (Wharton 2000:225). Because the term ‘vena jugularis interna’ can only be used after receiving several other branches on its route to the heart, we suggest the term not be used for the vein immediately leaving the braincase, preferring ‘vena cephalica posterior’ (which is

also preferred to ‘vena cerebralis posterior’; see Dendy 1909:413). In the same way, we would suggest the term ‘vagus foramen’ be preferred over ‘jugular foramen’.

The vena cephalica media (Figure 25A) is a major, but rather slender vein that originates from the transverse sinus and leaves the braincase through the trigeminal foramen (Bruner, 1908; Dendy 1909). This is the plesiomorphic condition for Archosauria, also found in Sphenodon (Dendy 1909; Säve-Söderbergh, 1947), the derived state being the partial or total subsequent bony subdivision into two foramina, one for the vein and another for the trigeminal nerve (Gower 2002). Extracranially, a branch arises from the vena cephalica media, termed the vena cerebralis media secunda, that extends from the anterior part of the trigeminal foramen ventrally, joining the vena capitis lateralis in front of the basisphenoid (Bruner 1908), and drains blood from the region of the hypophysis. Outside the braincase, the vena cephalica media opens into the vena capitis lateralis, which, after receiving other tributaries such as the vena tympanica and the vena cephalica posterior, will be then termed vena jugularis interna (O’Donoghue 1920). The anterior-most portion of the vena capitis lateralis (shortly before its junction with the vena cephalica media) is termed vena capitis medialis, and begins in the sinus orbitalis (O’Donoghue 1920). This vein has a less definite wall and bigger proportions, being almost a continuation of the sinus (Bruner 1908). Another tributary of the transverse sinus is the vena capitis dorsalis, which enters the braincase through a foramen lying at the junction between the parietal, supraoccipital, prootic, and laterosphenoid (Bruner 1908, Dendy 1909, Sampson & Witmer 2007). This vein is, in turn, formed by two other veins, “a lateral one which arises above the parotic process [paroccipital process], and a median one which has its origin above the lateral margin of the foramen magnum” (Bruner 1908:18). It has also a contribution from the vena parietalis.

Janensch (1936) stated that in *Brachiosaurus*, *Barosaurus*, and *Kentrosaurus*, a foramen for the vena cerebralis media perforates the medial surface of the supraoccipital not far from its upper margin and opens in the occipital region. This foramen would be connected through a groove to a lower one, situated just slightly above or confluent with the trigeminal foramen (Figure 25B). According to this study, the transverse sinus would be connected to the vena capitis lateralis through the lower foramen and to the vena capitis dorsalis through the upper one, and this latter vein is the continuation of the transverse sinus emerging in the occipital region, at the upper margin of the supraoccipital. Once in the supraoccipital, the channel extending from the upper foramen penetrates the bone posteriorly and somewhat laterally, and then bifurcates (Figure 25C). One expansion extends posteriorly and opens in a foramen in the occipital region, close to the upper margin of the base of the paroccipital process. The second one departs from the bifurcation laterally at a right angle, exiting the braincase laterally after a short distance. Our observations of the specimens MB.R.2387

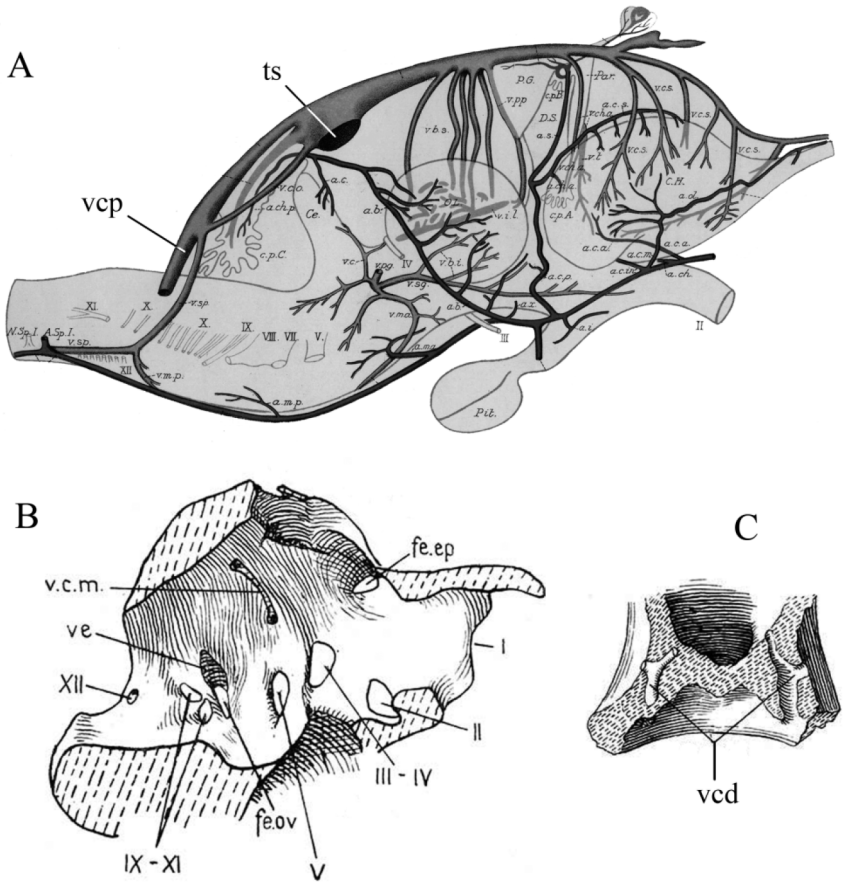

Figure 25: Cephalic veins identification and localization. A) Diagram of cerebral veins and arteries of *Sphenodon punctatus* in right lateral view; B) Left medial view of the braincase of *Barosaurus africanus* (MB.R.2387); C) transversal cut of the supraoccipital of *Kentrosaurus aethiopicus* (MB.R.3805) in dorsal view. ts: transversal sinus; vcd: vena capitis dorsalis; vcm: vena cerebralis media; vcp: vena cephalica posterior. A adapted from Dendy 1909; B and C adapted from Janensch 1936. For additional abbreviations, please refer to the original papers.

(*Barosaurus*) and MB.R.3805 (*Kentrosaurus*) suggest that Janensch's (1936) identification of the two foramina on the medial wall of the braincase of *Brachiosaurus* seems accurate despite the incorrect venous nomenclature. However, although Galton (1989), following his previous work on *Hypsilophodon* (Galton 1974), claims to have seen the same pattern as described by Janensch (1936) for *Brachiosaurus* in the braincase of *Dysalotosaurus*, we find it difficult to confirm his observations on the connection between these structures.

Moreover, CT scanning revealed the pathway of the vena capitis dorsalis within the supraoccipital/parietal suture (Figure 24), allowing identification of the internal and external openings of the vein. As previously noted, the internal opening of the vena capitis dorsalis lies on the ventral surface of the parietal just in front of the ventral projection of the supraoccipital, and the external opening lies on the suture line between supraoccipital and parietal. Thus, we interpret the upper foramen in *Dysalotosaurus* as the endolymphatic duct and not as a venous foramen. Likewise, Janensch's (1955) and Galton's (1989) statements

regarding the lack of a vena cerebralis posterior seem improbable; it probably left the braincase through the foramen magnum (see below).

On the Identification and Nomenclature of Cranial Nerve Foramina and the Presence of a Fenestra Pseudorotunda: Another subject of much misunderstanding involves the identification of the foramina located on the posterolateral surfaces of the braincase, namely those related to the middle ear and CN X–XII. Detailed discussion on the definition of the recessus scalae tympani, the division of the metotic foramen, and the implications for the nomenclature of these features has been provided by Rieppel (1985) and Gower & Weber (1998). According to Rieppel (1985), when the embryonic metotic fissure becomes divided by a bony structure, this leads to the formation of two chambers that connect to the exterior via foramina. The anterior chamber is the recessus scalae tympani, into whose lateral aperture the secondary tympanic membrane is attached, and which can also serve as the pathway for the glossopharyngeal nerve (CN IX), whose course is highly variable in reptile anatomy (Rieppel 1985). The posterior chamber is the passageway of the vagus nerve (CN X). Along with CN X, the accessory nerve (CN XI) (which is a secondarily independent ramus of CN X; Koch 1916; Starck 1982) and often the vena cephalica posterior might also be present. Based on this, Gower and Weber (1998) suggested the term ‘metotic fissure’ be used only for the embryonic structure, ‘metotic foramen’ for the plesiomorphically undivided condition, and ‘fenestra pseudorotunda’ when a secondary tympanic membrane is present.

Janensch (1955) labelled the three foramina on the posterolateral surface of the opisthothic as the nerves ‘IX + X’, ‘XI?’, and ‘XII’ (respectively, from anterior to posterior) and also mentioned that the middle foramen could indicate the exit of one branch of CN XII. Given the nature of the two posterior-most foramina, which pierce the braincase wall in a straight manner, and possesses virtually no connection with the otic area of the brain, it is reasonable to classify them both as exits for the anterior and posterior roots of CN XII. The identification of the anterior-most foramen, however, depends basically on the presence or absence of a fenestra pseudorotunda. Considering the possibility that a metotic foramen (undivided metotic fissure) was present in *Dysalotosaurus* implies that the foramen just behind the fenestra ovalis housed the exit of three cranial nerves (CN IX–XI) plus, probably, the vena cephalica posterior. This arrangement leaves the remaining foramen without a clear function. The description of Janensch (1955), however, suggests that he considered *Dysalotosaurus* to possess a subdivided metotic foramen and Galton (1989) agreed with this, despite misusing the nomenclature. In this scenario, the foramen behind the fenestra ovalis would be the fenestra pseudorotunda and our yet unnamed foramen would house the pathways of CN X (whether or not accompanied by CN IX and CN XI) plus the vena

cephalica posterior. What is intriguing is that this foramen does not seem to be large enough to house large structures like the CN X and the vena cephalica posterior (Säve-Söderbergh 1947), especially when comparing it to the size of the entrance of the cerebral branch of the carotid artery on the basisphenoid. This yet unnamed foramen of ours is similar in position to one identified in *Zephyrosaurus* as the perilymphatic duct (Sues 1980). However, the identification given by Sues (1980) implies a very strange inner ear morphology, because it would require the perilymphatic sac to lie posterior to the cranial nerves and have an internal, rather than medial, connection to the otic capsule. In addition, the perilymphatic duct would be directed coronally, instead of sagitally. A third possibility is that the metotic fissure was divided and that the unnamed foramen housed the exit of CN X but not the vena cephalica posterior. It could be that only a small branch of this vein left the braincase through the vagus foramen or not at all by this route, but through the foramen magnum instead, as sometimes occurs in *Ctenosaura* (Oelrich 1956) and crocodilians (Wharton 2000). Whereas cephalic arteries have very well defined paths and correlated anatomical features such as foramina, veins appear to be much more plastic (Oelrich 1956, Starck 1982, Walker 1990, Wharton 2000, Gower 2002) and are therefore not totally reliable for assumptions of homology and their relationships to anatomical landmarks. As noted by Gower (2002), this issue has been described confusingly with respect to diapsids and archosaurs in the literature.

To complicate the matter further, in suchians, when the vena cephalica posterior leaves the braincase through the lateral braincase wall, it does so by the dorsal end of the metotic foramen, where the bone can be pinched off to form a separate foramen for the passage of this vein (as suggested by Walker 1990, Gower 2002, Gower & Nesbitt 2006). On the posterior wall of the fenestra pseudorotunda there are three slight grooves above each other, which could indicate the paths of the cranial nerves and the vena cephalica posterior (although this last element is quite unlikely, given the issue of its thickness discussed above). The separation between the upper and the middle grooves is more strongly marked by a small portion of bone. Thus, it could be that the metotic foramen of *Dysalotosaurus* was undivided after all, but this conclusion would still leave the unnamed foramen without a clear function. Based on our observations and on our interpretations, we support the hypothesis that *Dysalotosaurus* very likely possessed a bony metotic strut (also termed ‘crista tuberalis’; for a short discussion on the structure and terms, see Sampson & Witmer 2007:68) separating the exit for CN X from the recessus scalae tympani. Moreover, given the complexity of the subject, we suggest that the posterior foramen formed by the bony subdivision of the metotic foramen be called the vagus foramen instead of the jugular foramen or any similar name.

Implications of Inner Ear Anatomy for the Behavior of *Dysalotosaurus* and the Phylogenetic Distribution of Characters: In general, in non-avian theropods the anterior semicircular canals are longer than the posterior and lateral ones (Sampson & Witmer 2007, Smith *et al*. 2011), which is also true for derived ornithopods (Evans *et al*. 2009) and ceratopsians (Witmer & Ridgely 2008a). This is not the case for *Dysalotosaurus*. Here, all three semicircular canals have roughly the same length, the lateral being slightly longer, and the posterior slightly shorter than the other two. Additionally, the posterior semicircular canal does not extend ventral to the lateral canal (in fact, it is placed slightly dorsal to it) and the anterior canal does not extend posterior to the common crus, in contrast to what is observed in *Archaeopteryx* (Dominguez-Alonso *et al*. 2004) or extant avialans (Witmer *et al*. 2008), where the anterior semicircular canal extends farther posteriorly. The lateral semicircular canal is positioned dorsally to the vestibule, as in other basal archosaurs (Sampson & Witmer 2009). The sizes of the semicircular canals are related to the movements of the eyes, head, and neck, and, in general, the longer the canal, the more sensitive it is to motion detection (Sampson & Witmer 2007; Witmer *et al*. 2008). The lateral canal of *Dysalotosaurus* is the longest of the three, and it is therefore possible that compensatory movements for quicker lateral turning of the head were more important for its behavior than vertical or rotational movements. There is also a relationship between the orientation of the lateral semicircular canal and the alert posture of the head (De Beer 1947, Duijm 1951, Witmer *et al*. 2003). When in such an alert posture, many vertebrates position their head so that the lateral semicircular canal is placed roughly parallel to the horizontal stereotaxic plane. Thus, the anteroventral inclination of the lateral semicircular canal of *Dysalotosaurus* indicates a slightly dorsally oriented position of the head while in alert posture, with a corresponding angle of approximately 17°. Reports of this 'nose-up' position are uncommon in the literature (Blanks *et al*. 1972, Mazza & Winterson 1984, Calabrese & Hullar 2006), and in fossil taxa it has been reported only for the sauropodomorph dinosaur *Massospondylus* (Sereno *et al*. 2007), whereas in most other fossil taxa studied, a horizontal or downturned alert position was recorded (Witmer *et al*. 2003, 2008; Sampson & Witmer 2007; Sereno *et al*. 2007). The cochlea is not strongly anteriorly or anteroventrally directed as in derived theropods or lambeosaurines, and it is not particularly elongate when compared to the remaining structures of the inner ear. A relatively short cochlea is also characteristic for sauropods (Witmer *et al*. 2008), whereas derived theropods, ceratopsians, and hadrosaurids and extant avialans and crocodilians have a more elongated cochlea. Taking into account the information available for the above clades as well as for *Euparkeria* (Gower & Weber 1998), *Erythrosuchus* (Gower 1997), and *Batrachotomus* (Gower 2002), we mapped the cochlear length on a simplified archosaurian phylogeny based on Butler *et al*. (2008), Allain (2002), and Brusatte *et al*. (2010c) using Mesquite 2.75 (Maddison & Maddison

2011 – Figure 26). The result shows that, contrary to Witmer *et al*. (2008), a short cochlea represents the plesiomorphic condition for Dinosauria, as well as for Saurischia. In Ornithischia, however, the evolution of this feature is still ambiguous. This is certainly a preliminary approach to this issue, because the character states 'short' and 'long' are poorly defined and not well explored in any of the above-mentioned papers. There seems to be a difference between the cochlear lengths of these taxa, which were not possible to quantify. As more data become available for a wider range of ornithodiran taxa, this hypothesis can be better tested. Cochlear length is related to the extension of the sensory epithelium and thus linked to the increase of the auditory capacity, with particular respect to the discrimination between lowand high-frequency sounds (Wever 1978). Walsh *et al*. (2009) demonstrated that it is possible to use cochlear length to estimate the best hearing range and the mean hearing frequency of extinct taxa. Using their calculations, we were able to predict the sensitivity values for *Dysalotosaurus* (cochlear length 9.67 mm, basicranial length 36 mm). The mean best hearing was 2100 Hz, and the overall best hearing range was 3500 Hz (approximately 350–3850 Hz). Surprisingly, these values are similar to some of the highest values of crocodilians, and the lowest values of avialans, differing especially from the estimates found for passerines and owls. The results found for *Dysalotosaurus* closely resemble those of the avialans *Struthio* and *Ciconia*, a palaeognath and a basal neornithine, respectively (Livezey & Zusi 2007). Both the short cochlea and the lack of pneumatic cavities in the braincase suggest that *Dysalotosaurus* had no refined ability to discriminate between low- and high-frequency sounds. Furthermore, the statement of Walsh *et al*. (2009) that avialans can provide a better estimation of non-avian dinosaur auditory capacities must be considered carefully. Not all avialan clades are suitable for such comparisons, because avialans display a series of very to highly specialized features that may not correspond to the characters found in more basal clades of non-avian dinosaurs.

CONCLUSIONS

Investigation of the *Dysalotosaurus* braincase using high resolution X-ray computed tomography has permitted further description and correction of several previously misidentified inner ear and braincase structures, such as the path of the vena capitis dorsalis and the path of the endolymphatic duct. This reanalysis shows that *Dysalotosaurus* already possessed a full bony subdivision of the metotic foramen into a fenestra pseudorotunda anteriorly and a vagus foramen posteriorly. Furthermore, the latter structure should be referred to as 'vagus foramen' instead of 'jugular foramen', because (a) the formation of this foramen is unlikely to be connected to the pathway of the posterior cerebral vein, but rather to the vagus nerve; and (b) when leaving the braincase, the identification of this venous

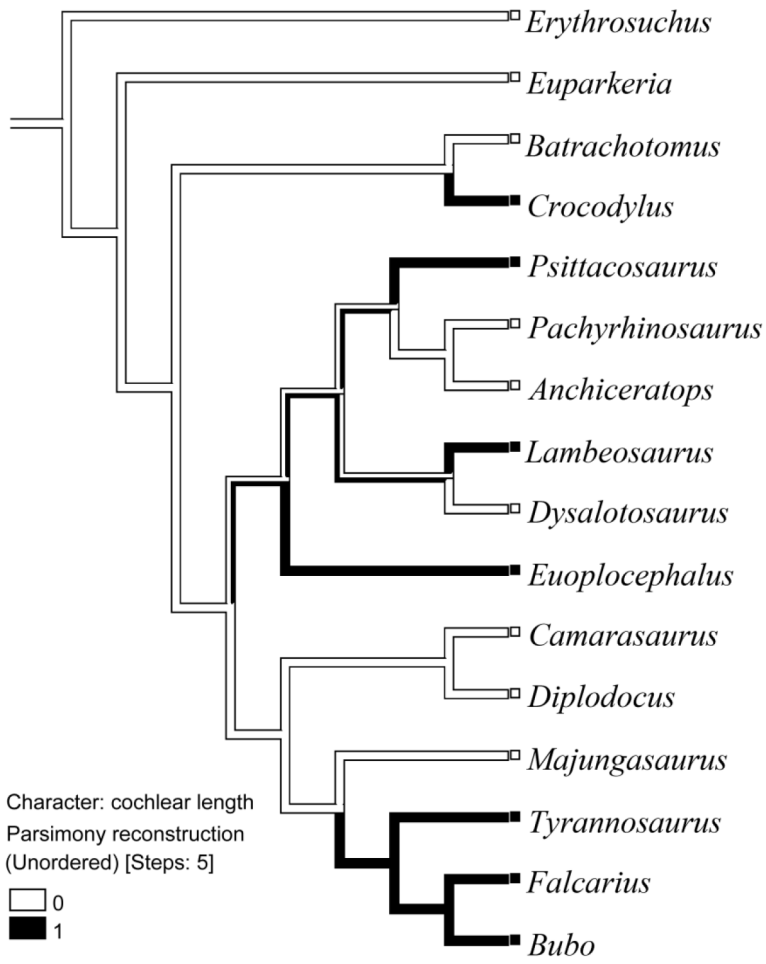

Figure 26: Optimization of the character 'cochlear length' (0, short; 1, long) on a simplified archosaurian tree. The taxon *Erythrosuchus* was used as the outgroup.

structure is better regarded as 'posterior cerebral vein' rather than 'jugular vein' (Großer & Brezina 1895, Dendy 1909, O'Donoghue 1920). The subdivision of the metotic foramen by a metotic strut is considered a derived feature and is usually associated with a more refined sense of hearing (Müller & Tsuji 2007), but is of unknown origin within crown group Archosauria. Basal archosauromorphs including *Euparkeria* (Gower & Weber 1998) and erythrosuchids (Gower 1997) do not possess a metotic strut, and neither do basal crurotarsans (Gower 2002, Gower & Walker 2002). The distribution of this character is also virtually unknown in basal clades of Ornithodira. The middle and inner ears of *Dysalotosaurus* bear many similarities to those of sauropod dinosaurs, and many differences from those of more derived theropods, hadrosaurids, and ceratopsians (Witmer & Ridgely 2008a, Witmer *et al*. 2008, Evans *et al*. 2009). Like *Camarasaurus* and *Diplodocus*, the fine discrimination of low frequency sounds appears not to have been important for *Dysalotosaurus*. Although a slightly up-turned head alert posture is not common, the condition seen in *Dysalotosaurus* is not strongly marked and could be treated as being

functionally horizontal, a feature usually found in animals that do not rely on their binocularity. When compared to other dinosaurs, as well as for nondinosaurian archosaurs for which data are available, the equally sized and thick semicircular canals and the short cochlea seems to represent the plesiomorphic state for Dinosauria. On the other hand, the appearance of the fenestra pseudorotunda is certainly a newly acquired feature in archosaurian evolutionary history. In this sense, both the middle and inner ears of *Dysalotosaurus* show a mosaic of plesiomorphic and derived characters, pointing out a more complex evolution of these structures than previously thought.

EARLY ARCHOSAURIFORM BRAINCASE EVOLUTION

When considering the evolutionary history of the diapsids leading up to archosaurs, many trends in braincase anatomy are recognisable. In order to try to evaluate braincase evolution in the group, comparisons will here be made between *Captorhinus* (Heaton 1979), *Youngina* (Evans 1987, Garnder *et al*. 2010), *Prolacerta* (Evans 1986), *Euparkeria* (Gower & Weber 1998) and *Sphenodon* (Säve-Södeberg 1947).

The braincase of *Captorhinus* is antero-posteriorly long and the braincase floor is flat, a pattern that is followed by *Youngina* (Figure 8C), *Prolacerta* (Figure 27) and *Mesosuchus* (Figure 11–13) braincases quite closely. In the latter two it is however possible to observe that the posterior region of the braincase floor becomes elevated, albeit subtly, as the basioccipital is short and tall. As a result, the occipital condyle is positioned more dorsally than the basal tubera. *Euparkeria* (Figure 15–18), in contrast, has a very short and tall braincase. It is also possible to observe that in basal taxa the para- and basisphenoid have a greater contribution to the braincase floor than the baisoccipital and that they gradually become restricted to the anterior region of the braincase, in particular the parasphenoid, while the basisphenoid tends to occupy the mid-portion of the ventral surface of the braincase floor. The occipital condyle becomes progressively more developed, along with the basal tubera and the basipterygoid processes. The processes of *Mesosuchus* and *Euparkeria* are strongly ventrally directed and much more developed than those of the other taxa. It is interesting to notice that the medial pharyngeal recess is already present and quite well developed in *Youngina*, although in *Mesosuchus* or *Euparkeria* they are still rather shallow. Overall, the basisphenoid becomes taller, but, at the same time, it also shows a decrease in its dorsal extension as the prootic expands anteriorly and forms most of the area ventral to the trigeminal foramen. The decrease in participation of the parabasisphenoid on the lateral braincase wall has been briefly discussed by Evans (1986).

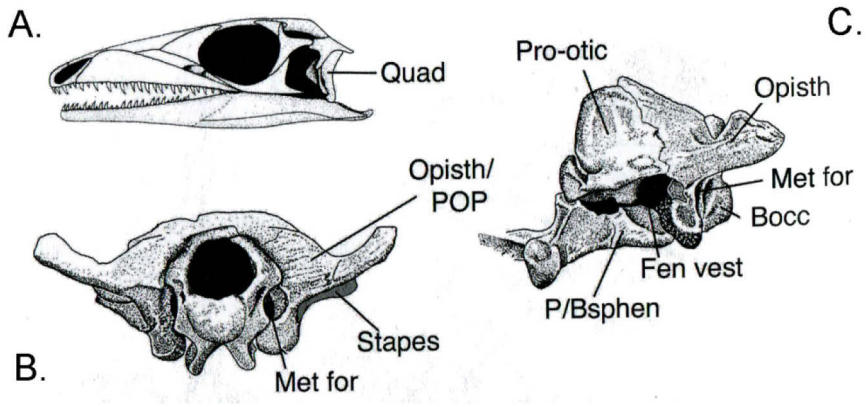

Figure 27: Prolacerta. A) skull in left lateral view; B–C) Briancase in posterior and left lateral view. Bocc: basioccipital Fen vest: fenestra vestibuli; Met for: metotic foramen; Opisth: opisthotic; POP: paroccpital process; P/Bsphen: parabasisphenoid; Q: quadrate. From Clack & Allin 2004.

The prootic is very short in *Captorhinus*, and much of the antero-dorsal portion of the braincase remained unossified. *Youngina* shows a significant increase in its development but, in comparison with other archosauromorph taxa, this extension is still limited. Also, with the development of the paroccipital process, the prootic becomes restricted to the anterior portion of its base. The paroccipital process itself becomes distally elongate and more dorso-posteriorly directed and located progressively more dorsally. In *Mesosuchus*, the well-developed cristae prootica and parotica, as well as the anterior border of the fenestra ovalis, form a recess in which the foramen of the CN VII is found, a pattern followed by *Euparkeria*. There is a change in the topographical relationships of the trigeminal and facial foramina and the fenestra ovalis: in *Captorhinus*, the nerves are closer together and the facial foramen lies dorso-anteriorly to the fenestra ovalis, close to the paroccipital process. In *Mesosuchus* and *Euparkeria*, however, the facial foramen is positioned more ventrally and more anteriorly relative to the paraoccipital process, while the facial foramen is also located further anteriorly. The stapes does not shorten, but becomes progressively more slender. In *Youngina* it still shows a perforating foramen, which has been lost in *Prolacerta*. The footplate of the stapes is also reduced in *Prolacerta*, and a delicate neck separates it from the remaining of the shaft. The opisthotic becomes taller, forming a proper lateral braincase wall. However, with the dominance of the exoccipital in the posterior region of the braincase, it also becomes restricted to the paroccipital process and to its ventral ramus. Like the prootic, the supraoccipital also shows an anterior extension and its dorsal surface becomes flat, although still dorsally directed. In *Captorhinus* and *Youngina*, the facial foramen is very small and, though absent in the *Prolacerta* specimen studied by Evans (1986), it is relatively more prominent in *Mesosuchus* and *Euparkeria* and the routes for its palatine and maxilla-mandibular branches are also more well-marked.

As the prootic, opisthotic and exoccipital become taller and develop the lateral braincase wall, certain posterior braincase elements such as the foramina of the CN XII and the metotic foramen rotate laterally and some inner ear structures such as the fenestra ovalis expands dorsally. In this regard, the morphology of *Meosuchus* is intermediate: its metotic foramen is laterally directed, but the foramina of the CN XII remain slightly posteriorly directed, as in *Captorhinus* or *Prolacerta*, but unlike *Euparkeria*. The elements forming the rims of the fenestra ovalis decrease in number. In *Captorhinus*, the rims of the fenestra ovalis are poorly ossified, but the parasphenoid, basisphenoid and basioccpital form much of its ventral, anterior and posterior borders. In *Youngina*, the fenestra is likewise poorly delimited, but it is formed only by the prootic and opisthotic. Both *Prolacerta* and *Mesosuchus* show a well-marked fenestra ovalis with no contribution from the baisoccipital, but in *Eupakeria* the basioccipital and parabasisphenoid contribute again to the postero- and antero-ventral borders of the fenestra. The metotic foramen becomes progressively more developed, and in *Captorhinus* it is formed by the opisthotic and basioccipital, but in *Youngina* the latter is substituted by the exoccipital. In *Prolacerta* it is unknown, but the pattern is followed by *Mesosuchus*. *Euparkeria* shows a further enlargement of the foramen, and the basioccipital takes part in its formation again, albeit restricted to its floor. Since the metotic foramen can to a certain extent act as a pressure-relief mechanism, its enlargement may indicate an increase in selective forces for the refinement of, and thus an improvement in, its hearing system.

The semicircular canals are elongate in *Euparkeria* in comparison to *Youngina*, but those of *Mesosuchus* are the longest and most slender of them. In *Youngina*, the lateral semicircular canal is the longest, conforming to basal amniotes and tetrapods in general, but in *Mesosuchus* and *Euparkeria* there is an evident development of the anterior semicircular canal. The common crus becomes also more dorsally positioned and as a consequence the utricculus becomes elongate. The vestibule of *Mesosuchus* seems to be more developed than that of *Euparkeria*, but the cochlea is much more elongate than in the latter.

PHENOTYPIC EVOLUTION

ANATOMICAL BACKGROUND

The characters selected to be plotted on archosaurian phylogeny (see below) include not only those related to impedance-matching hearing itself, but also to other parts of neuroanatomy. This decision was made after ascertaining how little attention the correct identifications of nervous, vascular, and pneumatic foramina have received – even less than general braincase anatomy itself. On the other hand, these are very important to assess the evolution of other sensory systems and, ultimately, the palaeobiology of extinct taxa and their ecosystem mechanics. During construction of the character list, it was noted that much of the evolution of the braincase is one way or the other related to its development – including the appearance of impedance-matching hearing. Therefore, before discussing each character in particular and its evolution, it is necessary to briefly describe the development of the skull in general. The relationships between the metotic fissure and fenestra pseudorotunda, cranial nerves and their branches, blood vessels, and embryonic structures are mostly conservative among diapsids. These constitute important landmarks in palaeontology for the identification of homologous structures as the braincase develops during the evolutionary history of archosaurs. The development of the lizard chondrocranium was thoroughly described by Gaupp (1900), later expanded by de Beer (1937), and more recently revised by Bellairs & Kamal (1981). The works of Rieppel (1985) and Gower & Weber (1998) represent the latest reviews concerning the development of the recessus scala tympani and the appearance of the fenestra pseudorotunda. The following description is based on Bellairs & Kamal (1981), Evans (2008), and Säve-Söderbergh (1947) on lepidosaurs, and archosaurian singularities were extracted from de Beer (1937) – unless indicated otherwise.

DEVELOPMENT OF THE BRAINCASE

Early in the development of the head, several independent elements of the chondrocranium are formed, including a pair of trabecular cranii, a pair of parachordals, a pair of otic capsules and a series of arches which are homologous to the vertebrae, located in the occipital region of the head (Figure 28A). The anterior portions of the trabeculae fuse early to form a trabecula comunis, which forms the basis of the nasal septum. The extent of the fusion is variable and may reach the orbital region, but the posterior ends of the trabecula cranii remain separate, forming a space termed pituitary or hypophyseal fenestra, which encloses the hypophysis (or pituitary gland – Figure 28B In this region, each trabecula develops a lateral process, which will ossify as the basipterygoid processes after contributions of the lateral wings of the parasphenoid. The parachordals are parallel bars

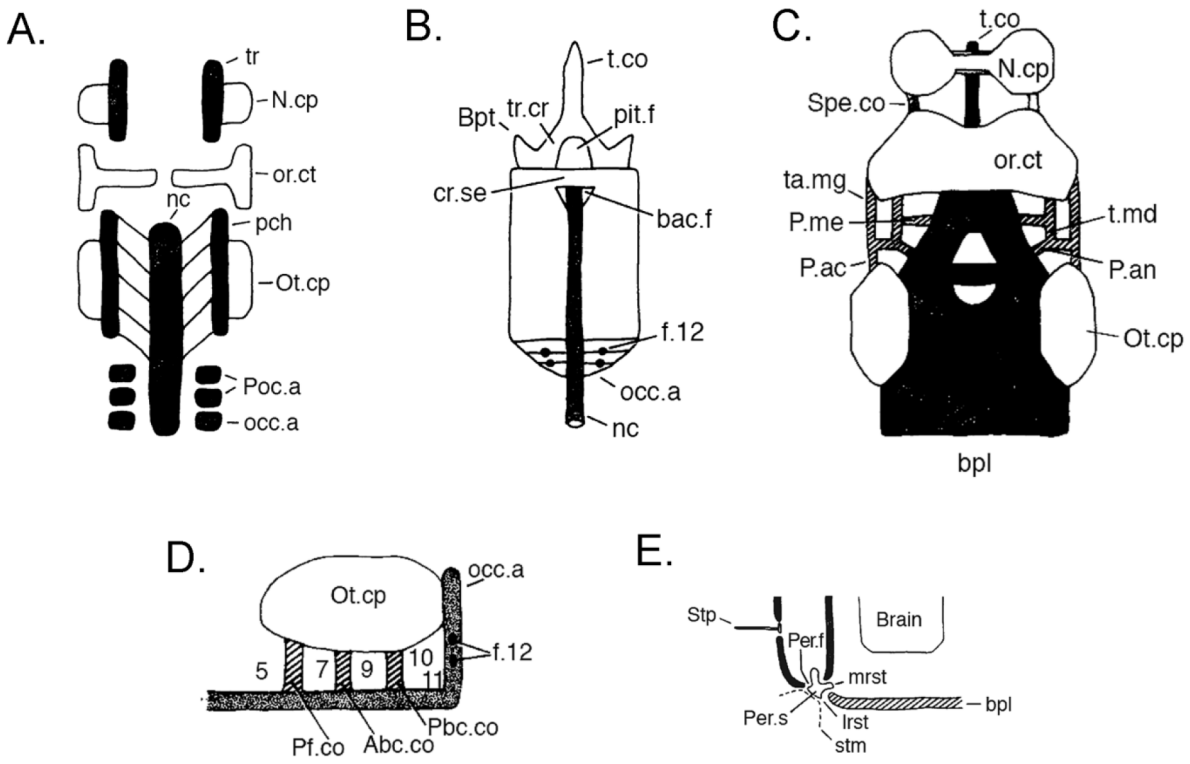

Figure 28: Schematic drawings of the development of the lizard chondrocranium. A) Early stage; B) Basal plate and sphenoid complex; C) Dorsal view of late stage; D) Left lateral view of the connections between otic capsule and basal plate; E) Coronal section of otic capsule at the region of the recessus scala tymapni. Abc.co: anterior basicranial commissure; bac.f: basicranial fenestra; bpl: basal plate; Bpt: basipterygoid process; cr.se: crista sellaris; lrst: lateral aperture of the recessus scalae tympani; mrts: medial aperture of the recessus scalae tympani; N.cp: nasal capsule; nc: notochord; or.ct: orbital cartilage; occ.a: occipital arch; Ot.cp: otic capsule; P.ac: pila accessoria; P.an: pila antotica; P.me: pila metoptica; Pbc.co: posterior basicranial commissure; pch: parachordal; Per.f: perilymphatic foramen; Per.s: perilympahtic sac; Pf.co: pre-facial commissure; pit.f. pituitary fossa; Poc.a: pre-occipital arches; Spe.co: sphenethmoid commissure; stm: secondary tympanic membrane; t.co: trabecula comunis; t.md: taenia medialis; ta.mg: taenia marginalis; tr: trabecule; tr.cr: trabecula cranii. Arabic numerals: foramina of corresponding cranial nerves. Modified from Evans 2008.

positioned more posteriorly, lying on each side of the notochord and fusing to form the basal plate. Subsequently, the posterior region of the trabeculae cranii and the anterior region of the basal plate fuse. In the region posterior to the hypophyseal fenestra, another opening is formed in the basal plate by means of re-absorption of existing cartilage, the basicranial fenestra (Figure 28B). Both fenestrae are separated from each other by the crista sellaris, which will later form the posterior wall of the hypophyseal fossa and the dorsum sellae. The cerebral branches of the internal carotid artery enter the brain cavity through the posterior region of the hypophyseal fenestra, and may pierce the base of the crista sellaris. Concomitantly, the preoccipital and occipital arches join together, extending ventrally to fuse with the basal plate. The separations of these arches are marked by the roots of the hypoglossal nerve (CN XII).

Meanwhile, the orbital cartilages fuse along the midline and form the planum supraseptale, which supports the forebrain. In the anterior region of the braincase, a connection between the otic capsule and the planum supraseptale is formed by means of a lateral taenia marginalis (Figure 28C). Another medial extension is developed from the planum supraseptale, the taenia medialis (sometimes called the taenia parietalis media), to connect to the basal plate through two vertical bars: the anterior pila metoptica extends medially and the posterior pila antotica (sometimes also termed pila prootica) extends laterally. A connection between the taenia medialis and the taenia marginalis is made by the pila accessoria. The optic nerve (CN II) leaves the brain cavity anterior to the pila metoptica, the oculomotor and the trochlear nerves (CN III and CN IV) exit between the pila metoptica and the pila antotica, and the trigeminal nerve (CN V) runs between the pila antotica and the otic capsule. The abducens nerve (CN VI) runs dorsal do the basal plate, grooving or piercing it close to the connection with the pila antotica. Alternatively, the foramina of the CN VI may traverse the dorsum sellae.

In many diapsid taxa, the anterior region of the braincase remains unossifed, being formed by a system of cartilage bars and membranous areas termed fenestrae by Gaupp (1900). This terminology has, however, led to some points of confusion in the literature, since these areas are not necessarily open, like a fenestra ovalis, but are usually membrane-filled and traversed by cranial nerves and blood vessels. Thus, the area anterior to the pila metoptica, through which passes the CN II, is termed fenestra optica. Likewise, there are the fenestra metoptica and the fenestra prootica, for the CN III and IV, and the CN V respectively. The oculomotor foramen is located in the center of the fenestra metoptica, while the narrower trochlear foramen is dorsal and slightly medial to it. The fenestra metoptica also transmits circulatory elements, such as the pituitary vein and the ophthalmic artery – which degenerates in many avialans and is replaced by the sphenoidal or sphenopalatine artery (Witmer & Ridgely 2008a). They are usually transmitted together with the cranial nerves, but may present their own foramina. The foramina for cranial nerves III and IV may also converge and exhibit only a single opening. In extant crocodilians, and also in some dinosaur taxa, the foramen of the CN III has a more ventral position as the fenestra metpotica becomes sub-divided, separating the oculomotor from the trochlear nerve (Sampson & Witmer 2007), and may being confluent with the foramen of the CN VI.

The inner ear develops within the otic capsule, which is, at first, not connected to the basal plate. The otic capsule expands dorsally to enclose the semicircular canals, and its ventro-lateral wall includes the large opening of the fenestra ovalis. Openings for the vestibulocochlear, or auditory, nerve (CN VIII) and for the passage of the endolymphatic sac into the brain cavity are present on its medial wall, and ventrally on its floor, the perilymphatic foramen leading from the cochlear cavity. A ridge marks the bulging area of the lateral

semicircular canal and is termed crista parotica. The fusion between the otic capsule and the basal plate is provided by means of ventral connections called commissures (Figure 28D). The prefacial commissure separates the trigeminal (CN V) and facial nerve (CN VII) ganglia. Posterior to the CN VII ganglion, the basicranial (or basicapsular) commissure is formed and, posterior to it, the otic capsule is separated from the basal plate by a space called the metotic fissure. The posterior end of the fissure is delimited by the contact of the posterior part of the otic capsule with the anterior tip of the occipital arch. The anterior part of the metotic fissure contains the recessus scalae tympani (Figure 28E). It is connected to the otic capsule by the perilymphatic foramen antero-dorsally, to the cranial cavity and to the middle ear cavity – both by foramina called either (medial/lateral) jugular or metotic foramina. More posteriorly, through the metotic fissure, the cranial nerves IX, X and XI plus the posterior cerebral vein leave the braincase into the middle ear region.

The regionalization of the embryonic metotic fissure can become physically separated by the concentration of connective tissue (Gaupp 1900) or by the apposition of the otic capsule to the basal plate (Bellairs & Kamal 1981) between the CN IX and the remaining neural and vascular elements (this new connection between otic capsule and basal plate is termed posterior basicapsular commissure and the one located behind the ganglion of the CNVII mentioned previously is named anterior basicapsular commissure – Figure 28D). Either way, there is the subsequent formation of the recessus scalae tympani *sensu stricto*, the fenestra pseudorotunda and the apertura medialis anteriorly, and the vagus passageway and medial and lateral foramina posteriorly. The glossopharyngeal nerve usually exits the braincase through the fenestra pseudorotunda (in some cases secondarily reduced as to allow only the exit of the nerve), but sometimes also through the vagus foramen. In the adult, this commissure is represented by the metotic strut – also referred to as ventral extension of the opisthotic. The space between the anterior and posterior basicapsular commissures (or the anterior and the occipital arch), is also known as basicapsular fenestra, and encloses both the recessus scalar tympani (or the metotic fissure) and the region of the cochlea. It will later become sub-divided by the basicochlear commissure and chondrify as the crista interfenestralis, which separates the fenestra ovalis from the fenestra pseudorotunda (or from the metotic foramen).

Archosaurian Pattern: In archosaurs, all the cartilaginous structures described above may ossify, or at least calcify, in different patterns and degrees. For instance, parts of the taenia medialis and the pila metoptica may ossify to form the orbitosphenoid, while the pila antotica contributes to the epipterygoid and to the laterosphenoid (previously also termed “pleurosphenoid”). The posterior ends of the trabeculae cranii, the crista sellaris, the basipterygoid processes and part of the basal plate will contribute to the formation of the

basisphenoid – which will in many cases fuse to the dermal element parasphenoid, together being often referred to as parabasisphenoid. During the fusion of the para- and basisphenoid ventral to the hypophyseal region, the internal carotid artery and the palatine branch of the facial nerve (CN VII_{pal}) become enclosed in the vidian canal, which passes through the base of the basipterygoid process either laterally or ventrally. The development of the otic capsule in archosaurs is overall similar to that of lepidosaurs, as their metotic fissure also becomes subdivided, forming a true recessus scalae tympani. However, the morphology of the fully developed capsule varies between avialans and crocodilians. Furthermore, the homology of the process by which the subdivision occurs is still not confirmed (Rieppel 1985).

The overall morphology of the ear region of Crocodylia is very peculiar. The quadrate abuts directly against the lateral wall of the braincase, and the posteriormost region of the basioccipital does not face ventrally, but posteriorly instead. Both the fenestra ovalis and the fenestra pseudorotunda lie anterior to the abutting point, and thus remain concealed laterally by the medial wing of the quadrate. The vagus foramen, on the other hand, opens posteriorly, just lateral to the exit of the CN XII and the foramen magnum. Furthermore, the subdivision of the metotic fissure is not complete, and thus on the medial wall of the otic capsule a common metotic foramen for the exit of the cranial nerves IX – XI and the posterior cerebral vein still persists in the adult (Figure 9B). This partial subdivision is considered to be formed by an extension of the lateral surface of the occipital arch dorsal to the hypoglossal foramina, called subcapsular process, which is similar to the pattern of lepidosaurs.

In Aves, on the other hand, the sub-division occurs by the formation of a metotic cartilage – the problem being the homologization of the metotic cartilage and the subcapsular process. The metotic cartilage connects the lateral wall of the otic capsule to the occipital arch, forming the lateral and posterior walls of the recessus scalae tympani. Morphologically, the recessus is more similar to that of lepidosaurs, with the fenestra pseudorotunda directed not laterally, but posteriorly into the metotic fissure.

MATERIALS & METHODS

The anatomy of the otic region of avialans and crocodilians, especially in regard to the presence of the fenestra pseudorotunda, had been suggested to be homologous (de Beer 1937, Whetstone & Martin 1979) – and although this hypothesis was questioned (Gower & Weber 1998, Rieppel 1985), it had never been properly tested. Investigations performed here were made through literature survey and through anatomical examinations derived from first-hand observations of key fossil taxa. As already mentioned, special

emphasis was given on the morphology of the middle and inner ears, but other aspects of braincase anatomy, in particular related to the neuroanatomy, were considered.

TAXON SELECTION

The braincase is not a particularly abundant component of fossil specimens, and thus descriptions are relatively rare, so all available information was considered as much as possible. However, descriptions are very often superficial and incomplete, and in many cases structures were incorrectly identified. Therefore, some taxa were selected for first-hand analysis. As usual, financial reasons constrained the number of collections to be visited so that taxa were selected according to two criteria: the availability of the material and their phylogenetic significance. Priority was given to basal members of each clade, in an attempt to correctly reconstruct the ancestral states of the characters without the interference of phenomena like long-branch attraction. When coding, I used my own interpretations for the identification of structures, both when materials were analysed first hand and when information was extracted from the literature. A list of materials analysed, as well as papers used are listed in Table 1.

CHARACTER SELECTION

As the focus of this work is impedance-matching hearing in archosaurs, the presence of a fenestra pseudorotunda was the main character surveyed. Furthermore, since braincase anatomy has been largely neglected in the literature, focus was given to it and not to the temporal region of the skull. The recognition of osteological correlates of soft tissue anatomy has been an important source of information for the reconstruction of the physiology, ecology and behaviour of fossil taxa – and ultimately, of past ecosystems – that has been in evident growth (Witmer *et al*. 2008). A list of characters to be surveyed was made based on Clack (1998), Gower (2002), and Gower & Weber (1998), but also on personal observations. Due to the anatomical context the characters chosen have with other braincase structures and to braincase evolution, and also to facilitate reading, the complete list of characters is given in the next section, followed by a brief introduction and discussion of the results.

SUPERTREE

Methods of taxonomic congruence, or consensus methods, were developed early in the history of phylogenetic systematics in order to unify different relationship hypothesis based only on the tree topology (Adams 1972, Kluge 1989). However, when comparing trees derived from different studies, not infrequently they did not contain the same sub-set of taxa, and Gordon (1986) developed a method termed supertree to overcome this problem.

Table 1: List of taxa with corresponding reference, collection number and institution.

Taxon	Reference	Material	Institution
Adeopapposaurus	Martínez 2009	PVSJ 568, PVSJ 610	Instituto y Museo de Ciencias Naturales de la Universidad Nacional de San Juan
Aetosauroides	-	PSVJ 326	Instituto y Museo de Ciencias Naturales de la Universidad Nacional de San Juan
Alioramus	Bever *et al*. 2013	-	-
Almadasuchus	Pol *et al*. 2013	-	-
Ampelosaurus	Knoll *et al*. 2013	-	-
Amurosaurus	Godefroit *et al*. 2004, Lauters *et al*. 2013	-	-
Anatosuchus minor	Sereno *et al*. 2003, Sereno & Larsson 2009	-	-
Apatosaurus	Balanoff *et al.*2010	-	-
Araripesuchus tsangatsangana	Turner 2006	-	-
Araripesuchus wegeneri	Sereno & Larsson 2009		
Arizonasaurus babbitti	Gower & Nesbitt 2006	-	-
Barosaurus	Janensch 1935	MB. R. 2388	Museum für Naturkunde Berlin
Baryonyx	Charig & Milner 1997	BNHM R9951	Natural History Museum
Batrachotomus kupferzellensis	Gower 2002	-	-
Brachiosaurus	Janensch 1935, Knoll & Schwarz-Wings 2009	MB.R. 2180.22.4, 2384.1, 2387	Museum für Naturkunde Berlin
Camarasaurus	Madsen *et al*. 1995, Witmer *et al*. 2008	-	-
Ceratosaurus	Sanders & Smith 2005	-	-
Cetiosaurus	Galton & Knoll 2006	-	-
Chasmosaurus	Lehman 1989	BNHM R4948	Natural History Museum
Citipati	Clark *et al*. 2002	-	-

Dakosaurus andiniensis	Pol & Gasparini 2009	-	-
Desmatosuchus haploceras	Small 2002	UCMP 27414, 27416, 27408, 27421	University of California Museum of Paleontology
Dibothrosuchus elaphros	Wu & Chatterjee 1993	-	-
Dicraeosaurus	Janensch 1935	MB.R. 2379	Museum für Naturkunde Berlin
Diplodocus	Witmer *et al*. 2008	-	-
Dromaeosaurus	Currie & Zhao 1993	-	-
Dysalotosaurus	Janensch 1955, Galton 1977, Galton 1983, Galton 1989, Sobral *et al*. 2012	MB.R.1373, 1370, 1372	Museum für Naturkunde Berlin
Effigia okeeffeae	Nesbitt 2007	-	-
Eocursor	-	SAM-PK-K8025	South African Museum
Erythrosuchus	Gower 1997	UCMZ T700, BP/1/3893	University of Cambridge Museum of Zoology, Bernard Price Institute for Paleontological Research
Euoplocephalus	Miyashita *et al*. 2011	-	-
Euparkeria	Gower & Weber 1998	SAM-PK-7696, 5867	South African Museum
Europasaurus	Marpmann *et al*. 2014	-	-
Falcarius	Smith *et al*. 2011	-	-
Geosaurus saltillense	Buchy *et al*. 2006	-	-
Giganotosaurus	Coria & Currie 2002	-	-
Gryposaurus	Prieto-Marquez 2010a	-	-
Hamadasuchus	Larsson & Sues 2007	-	-
Heterodontosaurus	Norman *et al*. 2011	SAM-PK-K1332, K337	South African Museum
Hungarosurus	Ösi et al 2014	-	-
Hypsilophodon	Galton 1974	BMNH R2477a	Natural History Museum
Iguanodon	-	BNHM R11521, R99, R5342	Natural History Museum

Incisivosaurus	Balanoff *et al*. 2009	-	-
Kentrosaurus	Galton 1988, Hennig 1915	MB. R. 3804, 3805, 3808, 3811	Museum für Naturkunde Berlin
Levnesovia	Sues & Averianov 2009	-	-
Lewisuchus	Bittencourt *et al*. 2014	PULR 01	Museo de la Universidad Nacional de La Rioja
Lirainosaurus	Díaz *et al*. 2009	-	-
Lomasuchus palpebrosus	Gasparini *et al*. 1991	-	-
Longosuchus meadei	Parrish 1994	-	-
Mahajangasuchus insignis	Turner & Buckley 2008	-	-
Mahakala	Turner *et al*. 2011	-	-
Majungasaurus	Witmer & Ridgely 2009	-	-
Malawisuchus	Gomani 1997	-	-
Mariliasuchus amarali	Zaher *et al*. 2007	-	-
Massospondylus	-	SAM-PK-K1325, K7904, 1314, BP/1/4376, 5276, 4779	South African Museum, Bernard Price Institute for Paleontological Research
Megalosaurus	-	BNHM R1946, R6775	Natural History Museum
Mesosuchus	-	SAM-PK-6536	South African Museum
Montanoceratops	Makovicky 2001	-	-
Mystriosuchus westphali	Hungerbühler 2002	GPIT 261/001	Paläontologische Sammlung der Eberhard Karls Universität Tübingen
Neoaetosauroides engaeus	Desojo & Báez 2007	-	-
Notosuchus terrestris	Fiorelli & Calvo 2008	-	-
Oviraptor	Clark et al. 2009	-	-
Pachyrhinosaurus	Witmer & Ridgely 2008a	-	-

Panoplosaurus	Pereda-Suberbiola & Galton 1994	-	-
Panphagia	Martínez *et al*. 2012	-	-
Pawpawsaurus	Lee 1996	-	-
Pelagosaurus typus	-	BNHM 32599, 33095	Natural History Museum
Piatnitzkysaurus	Rauhut 2004	-	-
Pissarrachampsa sera	Montefeltro *et al*. 2011	-	-
Plateosaurus	Prieto-Marquez & Norell 2011	PV 18318a, MB. R. 1937	Paläontologische Sammlung der Eberhard Karls Universität Tübingen, Museum für Naturkunde Berlin
Poekilopleuron	Allain 2002	-	-
Polacanthus	Norman & Faiers 1996	-	-
Postosuchus kirkpatrici	Weinbaum 2011	-	-
Postosuchus alisonae		-	-
Prestosuchus chiniquensis	Mastrantonio *et al*. 2013	-	-
Prolacerta	Evans 1986	SAM-PK-K10018, BP/1/2675	South African Museum, Bernard Price Institute for Paleontological Research
Protosuchus haughtoni	Busbey & Gow 1984	BP/1/4746, 4946	Bernard Price Institute for Paleontological Research
Protosuchus micmac	Sues *et al*. 1996	-	-
Psittacosaurus	Averianov *et al*. 2006	-	-
Purranisaurus cf. westermanni	Férnandez *et al*. 2011	-	-
Riojasuchus	Bonaparte 1971	PVL 3827, PVL 3828	Instituto Miguel Lillo
Saichania	Maryańska 1977	-	-
Saurosuchus galilei	Alcober 2000	PVSJ 32	Instituto y Museo de Ciencias Naturales de la Universidad Nacional de San Juan

Scelidosaurus	-	BNHM R1111	Natural History Museum
Shamosuchus djadochtaensis	Pol *et al*. 2009	-	-
Shatungosuchus hangjinensis	Wu *et al*. 1994	-	-
Shunosaurus	Chatterjee & Zheng 2002, Zheng 1996	-	-
Shuvosaurus inexpectatus	Chatterjee 1993, Lehane 2005	-	-
Silesaurus	Dzik 2003	-	-
Silvisaurus	Carpenter & Kirkland 1998, Eaton 1960	-	-
Simosuchus clarki	Kley *et al*. 2010		
Sphenosuchus acutus	Walker 1990, Gower & Weber 1998	SAM-PK-3014	South African Museum
Spinophorosaurus	Knoll *et al*. 2012	-	-
Stagonolepis robertsoni	Gower & Walker 2002	-	-
Stagonolepis olenkae	Sulej 2010	-	-
Steneosaurus pictaviensis	Wharton 2000	-	-
Struthiomimus	Makovicky & Norell 1998	-	-
Struthiosaurus	Pereda-Superbiola & Galton 1994	-	-
Talarurus	Tumanova 1987		
Tarbosaurus	Saveliev & Alifanov 2007	-	-
Tatankacephalus	Parsons & Parsons 2009	-	-
Tawa	Nesbitt *et al*. 2009	-	-
Tecovasuchus chatterjeei	Martz & Small 2006	-	-
Teleosaurus cadomensis	Jouve 2009	-	-
Telmatosaurus	Weishampel *et al*. 1993	BNHM R3387	Natural History Museum
Tenontosaurus	Winkler *et al*. 1997	-	-

Terrestrisuchus gracilis	Crush 1984	-	-
Thecodontosaurus	Benton *et al*. 2000	-	-
Thescelosaurus	Galton 1997	-	-
Tornieria	Remes 2006	MB.R. 2386	Museum für Naturkunde Berlin
Torvoneustes coryphaeus	Young *et al*. 2013	-	-
Troodon	Fiorillo *et al*. 2009	-	-
Turfanosuchus dabanensis	Wu & Russel 2001	-	-
Tyrannosaurus	Witmer & Ridgely 2009, 2010, Witmer *et al*. 2008	-	-
Zephyrosaurus	Sues 1980		

His method, however, did not accommodate conflicting hypotheses, a problem that was solved by Baum (1992) and Ragan (1992) independently with the Matrix Represetation with Parsimony method (MRP). The current definition of supertrees was given by Sanderson *et al*. (1998), where a supertree is the generation of an output tree derived from source trees with or without a total or partial overlapping set of taxa.

In supertrees the original matrices of the source trees are not considered, but rather only the topological information of the trees, so the methods are relatively less time–consuming than a supermatrix approach. A formal supertree approach approach has been broadly used in macroevolutionary studies (Brocklehurst *et al*. 2013, Ruta *et al*. 2011, Young *et al*. 2010). However, informal supertrees continue to constructed, especially when either extensive phylogenetic studies or less inclusive supertrees already exist for the group in question, and the production of a relationship hypothesis is not the main concern of the study (Benson & Choiniere 2013, Helmus *et al*. 2010). Given the recently published broad and partially overlapping studies covering several parts of archosauriform phylogeny, supertree construction methods were not necessary, and an informal supertree was assembled (Figures 29, 30) based on Bronzati *et al*. (*in prep*), Nesbitt (2011) and Müller *et al*. (2010), with particular sub-sets of the tree based on Bever *et al*. (2013), Brusatte *et al*. (2010c), Brusatte *et al*. (2013), Butler *et al*. (2007), Butler *et al*. (2014), Carrano *et al*. (2012), Ezcurra *et al*. (2010), Fiorillo & Tykoski (2012), Otero & Pol (2013), Parker (2007), Pol *et al*. (2013), Prieto-Marquez (2010b), Sampson *et al*. (2010), Thompson *et al*. (2012), Wu *et al*. (1997), Young & Andrade (2009), Zanno (2010), and Zaher *et al*. (2011).

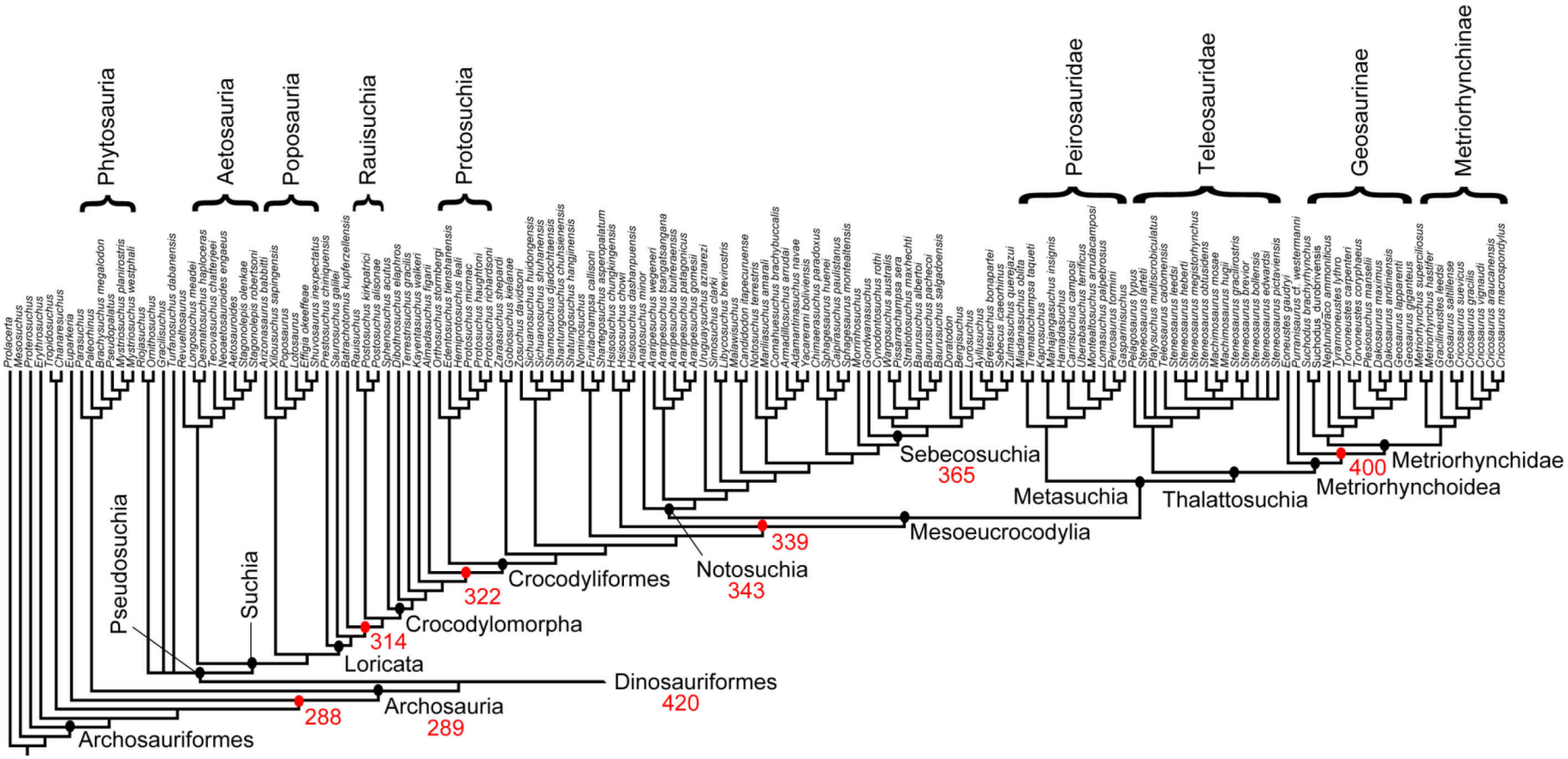

Figure 29: Supertree documenting the phylogentic relationships of basal archosauromorphs and pseudosuchians. See text for references. Numbers in red indicate nodes with significant changes in diversification rates (see next chapter for details). Relevant nodes for discussion in this and next chapters are named.

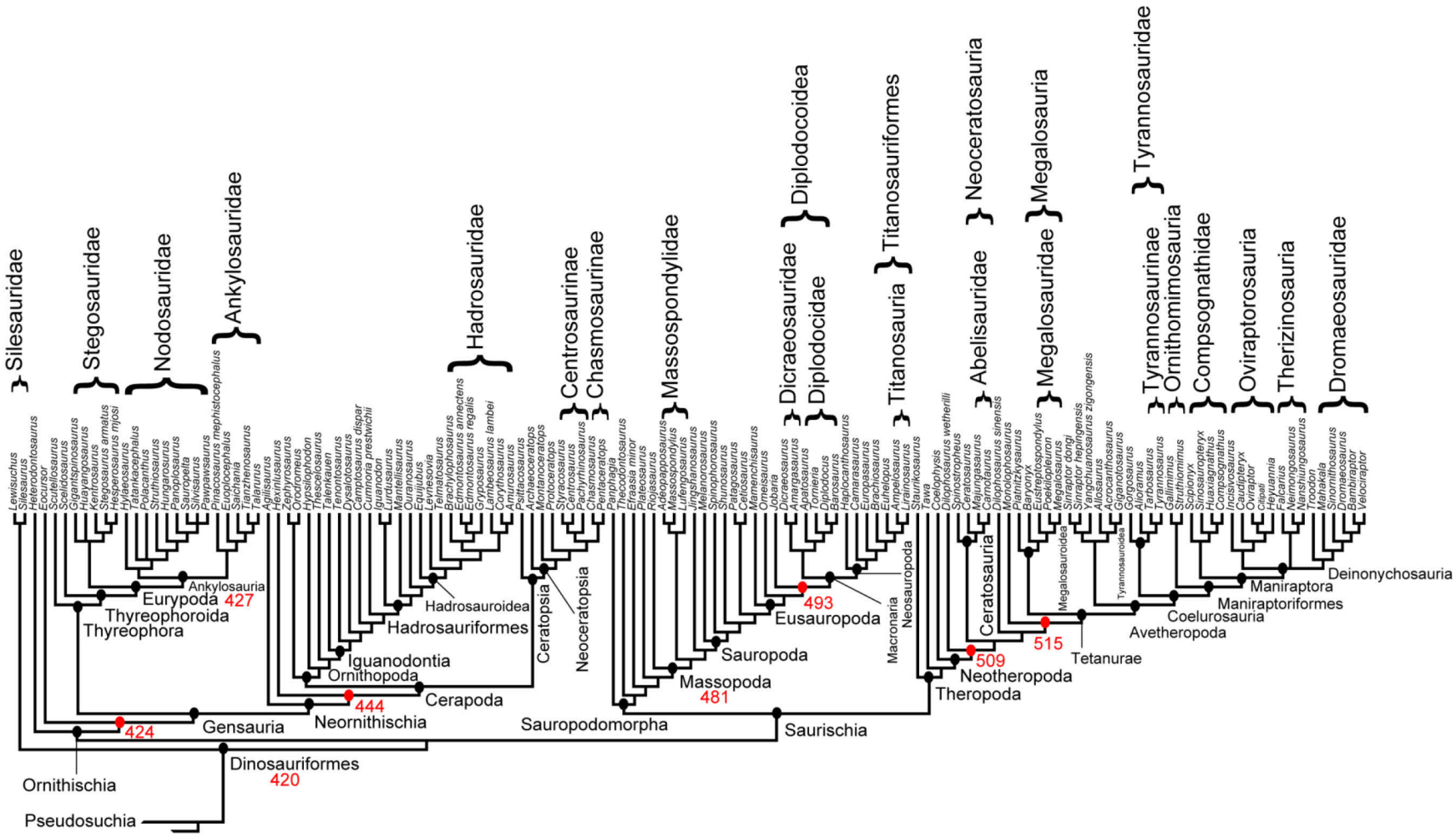

Figure 30: Supertree documenting the phylogentic relationships of dinosauriforms. See text for references. Numbers in red indicate nodes with significant changes in diversification rates (see next chapter for details). Relevant nodes for discussion in this and next chapters are named.

TIME CALIBRATION

The assembled tree was time-calibrated in order to identify not only when in evolutionary history a given character state appeared but also when it occurred in geological time (Figure 31, 32). The goal is to try to correlate two similar events taking place in different points of the cladogram with a geological or ecological event in time. Because of the inherent incompleteness of the fossil record, it is expected that the phylogenies will be but an approximate approach of the distribution of taxa through geological time. Thus, time calibrating a phylogeny is important for estimating ghost lineages and better correcting the time of first appearances of the characters studied. The phylogeny was time-calibrated using the stratigraphic occurrences of the various lineages available from Fossilworks (fossilworks.org). The function *Timescaling of Paleo-Phylogenies* (timePaleoPhy) of the "paleotree" (Paleontological and Phylogenetic Analyses of Evolution – Bapst 2012) package for the R statistical platform was used. Polytomies were not resolved and the time-scaling method used was the "basic" type, where nodes are as old as the first appearance of their oldest descendant. No node was given a minimum age.

ANCESTRAL STATE RECONSTRUCTION

This method is important for testing hypotheses of trait evolution. After coding the characters for the taxa available for study, the ancestral state correspondent to each node was calculated in order to predict when in the evolutionary history of the clades a given state first appeared. There are two main methods to calculate these reconstructions: parsimony- or likelihood-based mappings. Both methods were used here to reconstruct the states, but the mapping and evolution of the characters will be based on parsimony results. The reason for this is that the likelihood method was too conservative, and because only one-third of the tree could be scored, results were too scattered – i.e. all characters were highly homoplastic, appearing several times independently on each terminal branch for which they have been scored. In some cases the parsimony results were too generalized and the degree of uncertainty was equally high, but in a different way, with an unknown state for most of the phylogeny. Nonetheless, these results were still preferred over likelihood for actually being more plausible than several independent appearances, as will be discussed elsewhere. The parsimony method aims to minimize the number of character changes in order to explain character states shown by the terminal taxa given their proposed phylogenetic relationships. The reconstruction was carried out in Mesquite 2.73 build 544 (Maddison & Maddison 2011). Characters were treated as categorical and changes were unordered.

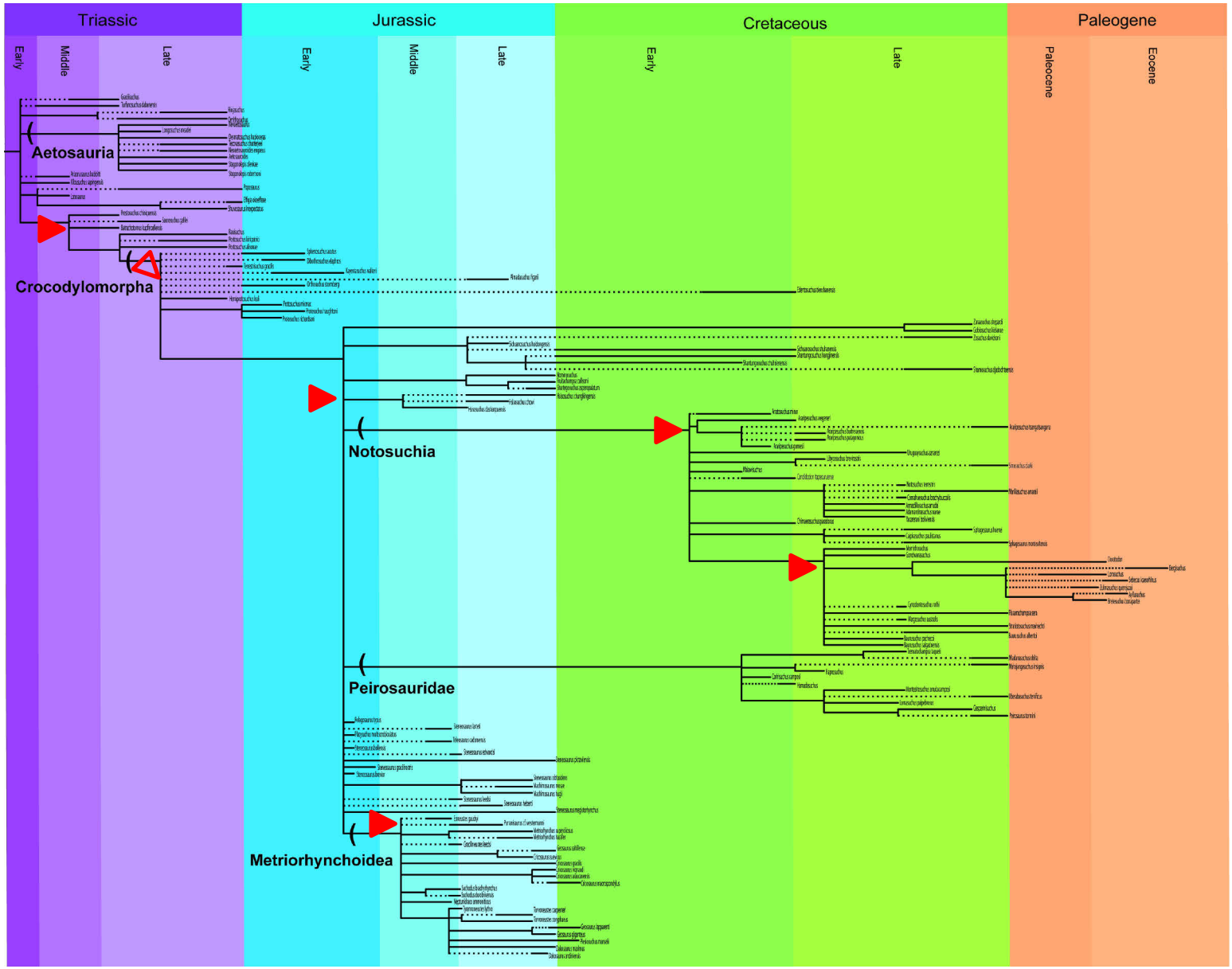

Figure 31: Time-calibrated tree of basal archosauromorphs and pseudosuchians. See text for methodological details. Dashed lines indicate ghost lineages. Temporal scale from the International Commission on Stratigraphy (http://www.stratigraphy.org). Red arrows indicate shifts in diversification (see next chapter for details).

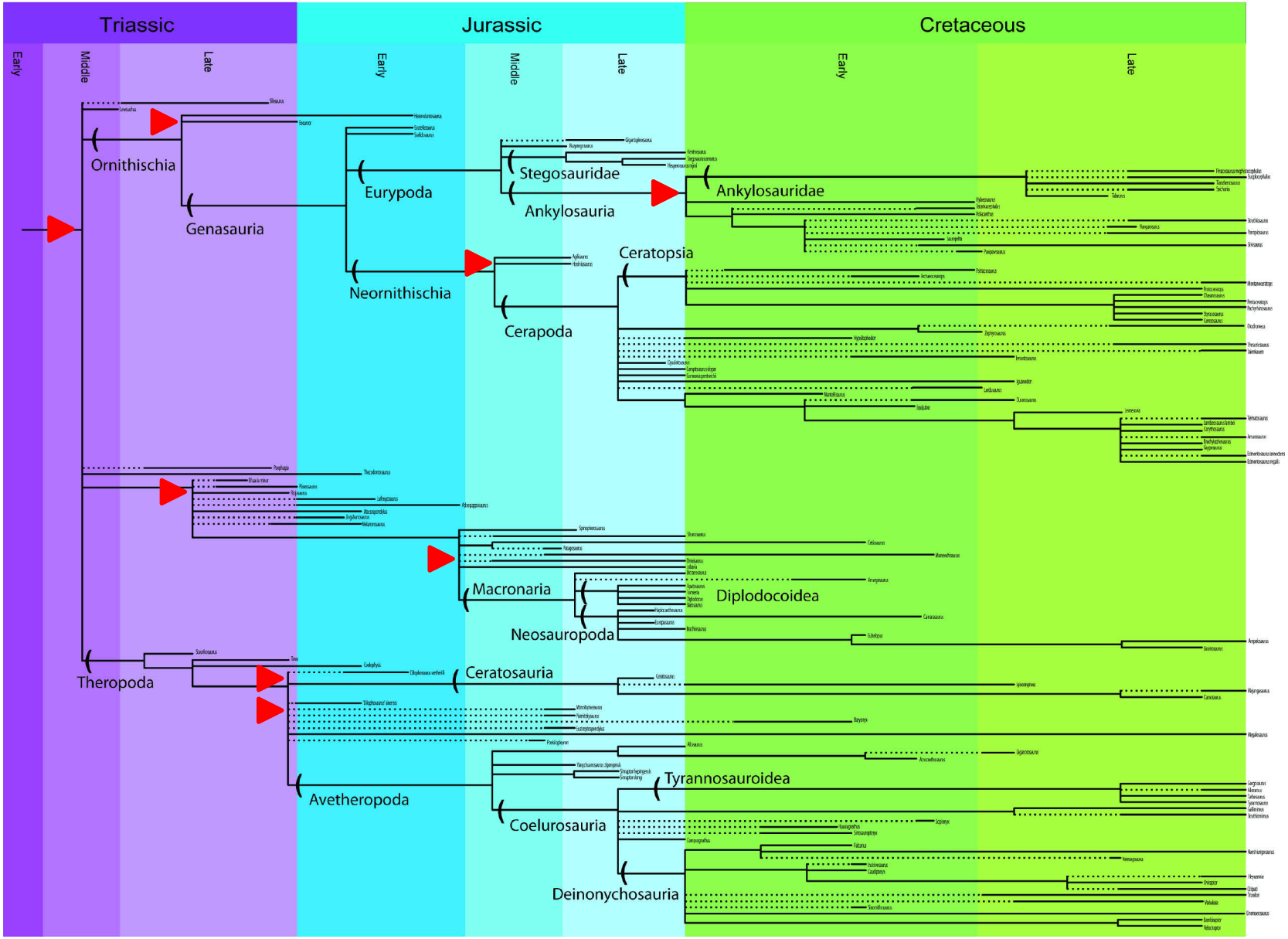

Figure 32: Time-calibrated tree of dinosauriforms. See text for methodological details. Dashed lines indicate ghost lineages. Temporal scale from the International Commission on Stratigraphy (http://www.stratigraphy.org). Red arrows indicate shifts in diversification (see next chapter for details).

Rates of Character Change: The evaluation of rates of character change per branch and per time was not initially planned, and tests were thus not performed. These are, however, interesting metrics of character evolution and will be considered for publication.

CHARACTER HISTORY

Although the topographical relationships of braincase bones and some of their structures are under-explored in the phylogenetic and macroevolutionary literature, characters here were selected according to their correlation to the appearance of impedance-matching hearing, as well as to the development and evolution of the braincase in general. This section is divided so that each character will be described, together with its different states and some further notes or a short summary on its general morphology. The results for the reconstruction of the ancestral states of each character are given along with their times of apperence and a brief discussion on their evolutionary history.

CHARACTER 1 – PAROCCIPITAL PROCESS ORIENTATION: LATERAL (0), OR POSTERO-LATERAL (1).

The stapes is connected to the tympanum through the extra-columella (Figure 2). In lizards, the extra-columella is held in place by the extracollumelar ligament and by the extracollumelar muscle.The ligament attaches to the cephalic condyle of the qudrate or to the paroccipital process, while the muscle attaches to the ceratohyal process. The post-tympanic band delimits the tympanic region posteriorly, attaching dorsally to the cephalic condyle and ventrally to the retroarticular process of the lower jaw. Many authors consider the quadrate conch and the retroarticular process as good indicators on the position of the tympanic membrane, but the orientation of the paroccipital process is rarely considered. The distal part of the process bears some relationship with the cephalic condyle, and proximo-ventrally it is excavated by the stapedial recess.

Optimization: The plesiomorphic state for the orientation of the paroccipital process was reconstructed as being postero-laterally directed in Archosauria. A change to a more laterally oriented process occurred in *Batrachotomus* during the Middle Triassic (MT), which could represent a state change in Loricata starting just prior to or after its branching off (Figure 33). However, such a state change certainly occurs in Crocodylomorpha in the Late Triassic (LT). A reversal occurrs in *Postosuchus kirkpatricki* (LT), *Terrestrisuchus* (LT), *Protosuchus micmac* (Early Jurassic, EJ), *Shantungosuchus hangjinensis* (Early Cretaceous, EC) *Anatosuchus* (EC), *Mahajangasuchus* (Late Cretaceous, LC) and *Pelagosaurus* (EJ) – and

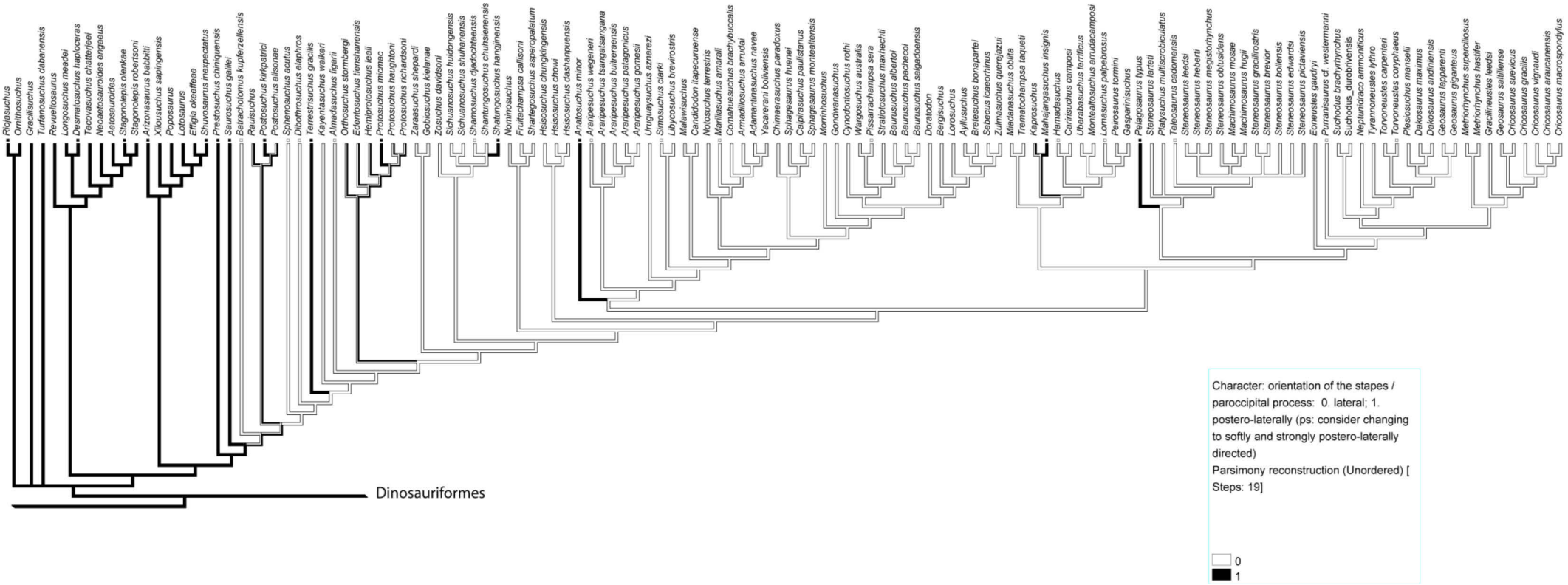

Figure 33: Optimization of character 1 for Pseudosuchia. Please refer to figure for character definition and character states.

might be plesiomorphic for Raiusuchia (LT), Protosuchidae (LT) and Mahajangasuchidae (EC) in general. In pseudosuchians, most of the state changes occurred during the Late Triassic.

A change to a lateral process occurs in certain terminal dinosauromorph taxa (for instance in *Lewisuchus* in the Middle Triassic), but the postero-lateral position remains plesiomorphic for Dinosauria (Figure 34). In Ornithischia, a reversal might have occurred early in Thyreophora in the Late Triassic, but certainly later in Ankylosauria during the Middle Jurassic – with a secondary change to the plesiomorphic state in *Hungarosaurus* (LC). In Neornithischia, this reversal happens independently in *Dysalotosaurus* (LJ), *Montanoceratops* (LC), and *Chasmosaurus* (LC). The last two could represent a reversal for Neoceratopsia (EC) and Chasmosaurinae (LC), respectively – in which case *Pachyrhinosaurus* would represent a further reversal to the plesiomorphic state within Neoceratopsia during the Late Cretaceous. In Saurischia, a potential reversal occurred later in Massopoda, starting *Jingshanosaurus* in the Late Triassic up to early Macronaria, where a reversal certainly occurred in *Camarasaurus* and *Brachiosaurus*, while *Europasaurus* retains the plesiomorphic state for sauropodomorphs – all during the Late Jurassic. In Diplodocoidea, the plesiomorphic postero-laterally directed process is found in *Dicraeosaurus*, but in *Barosaurus* it is lateral – also in the Late Jurassic. All these conflicting states are responsible for the uncertainty of state changes in this area of the tree. In Theropoda, a reversal occurs only in *Mahakala* during the Late Cretaceous, with no implications for state changes in the group. Most state changes for this character occurred in Sauropodomorpha during the Late Jurassic.

Discussion: While the direction of the paroccipital process is to a good extent linked to the position of the tympanic membrane, it seems most likely that the selective forces influencing its position are more related to other morphological or physiological processes, such as for instance the action of jaw and head muscles or level of cranial knesis. The action of temporal muscles can interfere with sound perception, and the development of dampening mechanisms can be advantageous (Wever 1978).

CHARACTER 2 – ANATOMY OF THE CN II FORAMEN: PAIRED FORAMINA FOR RIGHT AND LEFT BRANCHES (0), OR ONE SINGLE MEDIAL FORAMEN (1).

Technically, the optic nerve is but an anterior extension of the brain, but still called nerve by convention (Kardong 2001). It receives information from the retina and enters the braincase antero-medially through the fenestra optica, anterior to the pila metoptica. In cases where the anterior region of the braincase is ossified, it notches or pierces the latero- or the orbitosphenoid.

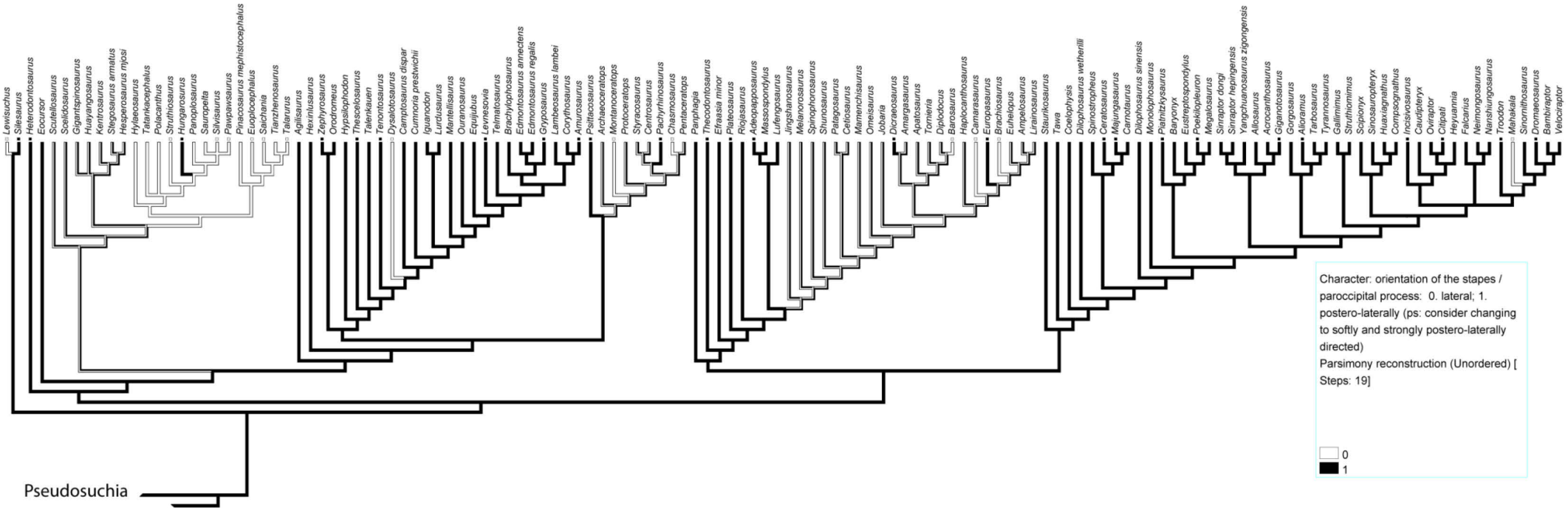

Figure 34: Optimization of character 1 for Dinosauriformes. Please refer to figure for character definition and character states.

Optimization: The plesiomorphic state is uncertain for Archosauria. The situation remains the same for early pseudosuchian clades (Figure 35), but starting with Aetosauria, during the Early Triassic, the plesiomorphic state is the presence of one single, medial opening for the nerve. The anatomy of this character is more plastic in Dinosauromorpha (Figure 36). The plesiomorphic condition was again impossible to reconstruct, but in Eurypoda (EJ), the presence of two foramina, a left and a right one, is the ancestral condition. In Neornithischia, the plesiomorphic state could also not be reconstructed, and the situation is unknown for almost the entirety of the group: *Tenontosaurus* (EC), *Levnesovia* (LC), *Gryposaurus* (LC), and *Montanoceratops* (LC) show one single foramen, while different foramina appear in *Iguanodon* (LJ), *Amurosaurus* (LC), and Ceratopsidae (LC). In Sauropodomorpha, the presence of two foramina is only known in *Plateosaurus* (LT), Diplodocoidea (LJ), and *Camarasaurus* (LJ), whereas a single foramen is present in *Shunosaurus* (MJ), *Cetiosaurus* (MJ), and in Macronaria starting with *Europasaurus* (LJ). In Theropoda, the plesiomorphic state is also unknown. *Ceratosaurus* (LJ) shows one single foramen while *Majungasaurus* (LC) and *Giganotosaurus* (LC) show two. However, for Coelurosauria (MJ), the presence of a single foramen is the ancestral condition, with a possible reversal within Oviraptorosauria in the Early Cretaceous – *Incisivosaurus* has two foramina, but *Citipati* has only one.

Discussion: As far as I am concerned, there is currently no indication that the presence of one single root or two different ones for the nerve is connected to its degree of development and to the importance of vision for a given group – although studies on the correlation of foramen size and nerve size indicate that these are good predictors for inferences on sensory receptor density (Muchlinski 2008, 2010). However, it seems to be no coincidence that in pseudosuchians the morphology of the nerve is more conservative, while in dinosaurs it is a lot more plastic – for two reasons. First, since avialans are known to be a group with such highly developed sight that the *bauplan* of the skull is often regarded as directly correlated to it (Bolk 1936, Starck 1979), it is not surprising that closely related groups were already under different selective forces resulting in different degrees of development of the nerve. Second, on the other hand, it might be that a plastic morphology may be a plesiomorphy not registered in the fossil record as the anterior region of the braincase does not become ossified until later in diapsid evolutionary history. Therefore, the morphology seen early in pseudosuchians might actually be a result of already acting forces in lower jaw adductor muscles and braincase morphology. Furthermore, even if not directly connected to an increase in importance of vision, the orbitotemporal region is the place of origin of many of the eye muscles, so that perhaps a role in sight might also be measured by

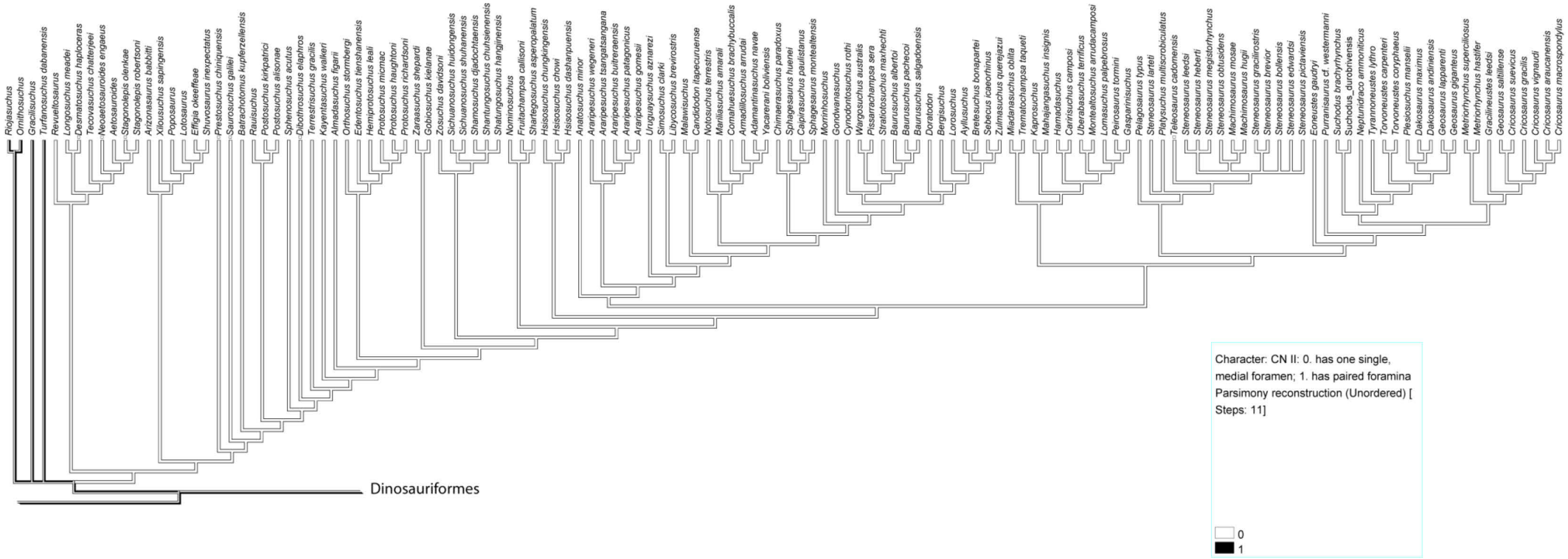

Figure 35: Optimization of character 2 for Pseudosuchia. Please refer to figure for character definition and character states.

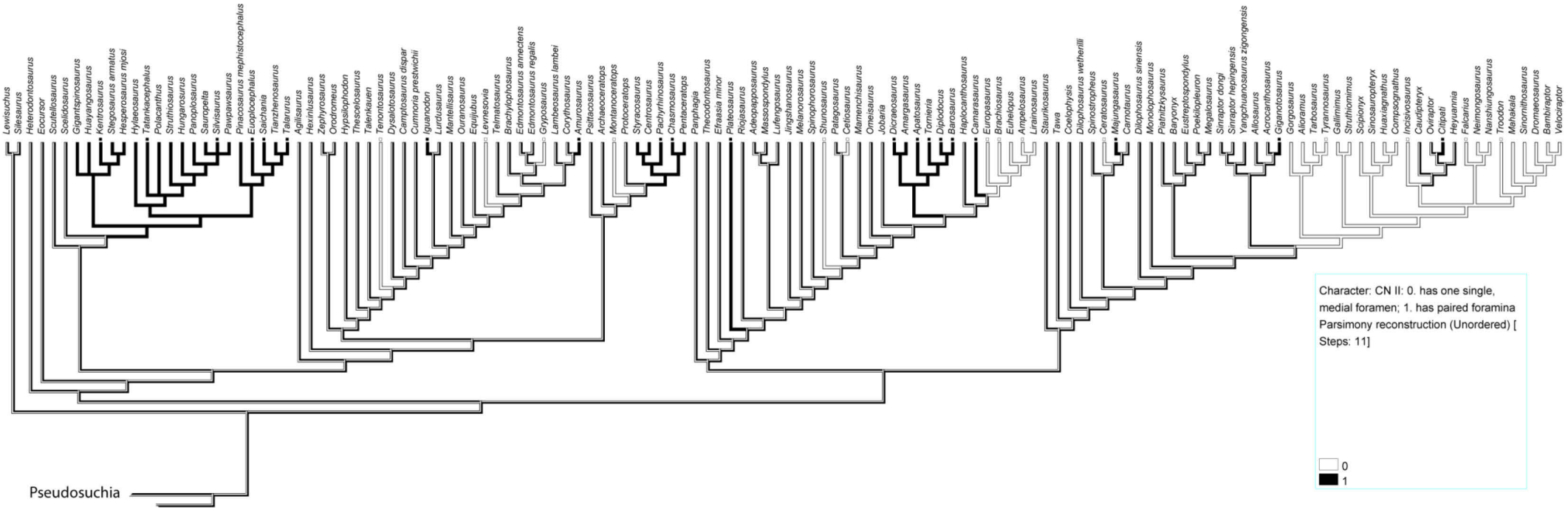

Figure 36: Optimization of character 2 for Dinosauriformes. Please refer to figure for character definition and character states.

the development of these muscles and the resulting arrangement of other anterior braincase elements – in which case would not be correlated only to the optic nerve, but also to the oculomotor and trochlear nerves and to the degree of ossification of the anterior braincase wall (see below). As a matter of comparison, in avialans there is usually one single foramen for the optic nerve, although the thin orbital septum may divide it in two (Baumel 1993). In contrast, the anterior-most region of the braincase of crocodilians is not ossified, but the laterosphenoid bears a notch on its anterior edge (Iordansky 1973). I would suggest that this indicates two separate foramina for the CN II, but I found no direct confirmation for this.

CHARACTER 3 – ANATOMY OF THE CN III AND CN IV FORAMINA: SEPARATE FORAMINA (0), OR CONVERGENT FORAMINA (1).

The oculomotor and the trochlear nerves are both motor nerves connected to eye muscles – not only of the eyeballs as a whole but also of the iris, ciliary body and eyelid (Kardong 2001). They are usually very small and exit the brain cavity through the fenestra metoptica, between the pila metoptica and the pila antotica. When separated, the oculomotor foramen is usually located at the center of the fenestra, while the trochlear foramen is usually positioned dorsal and slightly medial to the latter.

Optimization: The presence of two separate foramina for the oculomotor and trochlear nerves is plesiomorphic for Archosauria, and is widespread throughout the tree (Figure 37, 38). However, a confluent foramen occurs only in certain terminal taxa such as *Neoaetosauroides* (LT), *Levnesovia* (LC), *Shunosaurus* (MJ), *Barosaurus* (LJ), *Ceratosaurus* (LJ), and Titanosauriformes (LJ). The situation is unknown in Ankylosauria, where a confluent foramen might have appeared independently in *Tatankacephalus* (EC), *Silvisaurus* (EC), and *Euoplocephalus* (LC), or, alternatively, a reversal occurred in *Polacanthus* (EC) and *Saichania* (LC). Uncertainty also occurs in Allosauroidea, where *Giganotosaurus* (LC) shows only one foramen.

Discussion: As mentioned above, convergence in foramina has not been demonstrated to be correlated with size of the nerve roots nor to a higher or lower degree of development of the nerves, but it might bear some connection to the arrangement of anterior braincase elements and to the importance of the eyes in the biology of an animal. Even with an increase in importance of the vision, it is expected some development of the optic nerve (perhaps in size) but not so much of the trochlear or oculomotor nerves. They are not sensory nerves and, as important as the eyes may be, there is only a limited array of

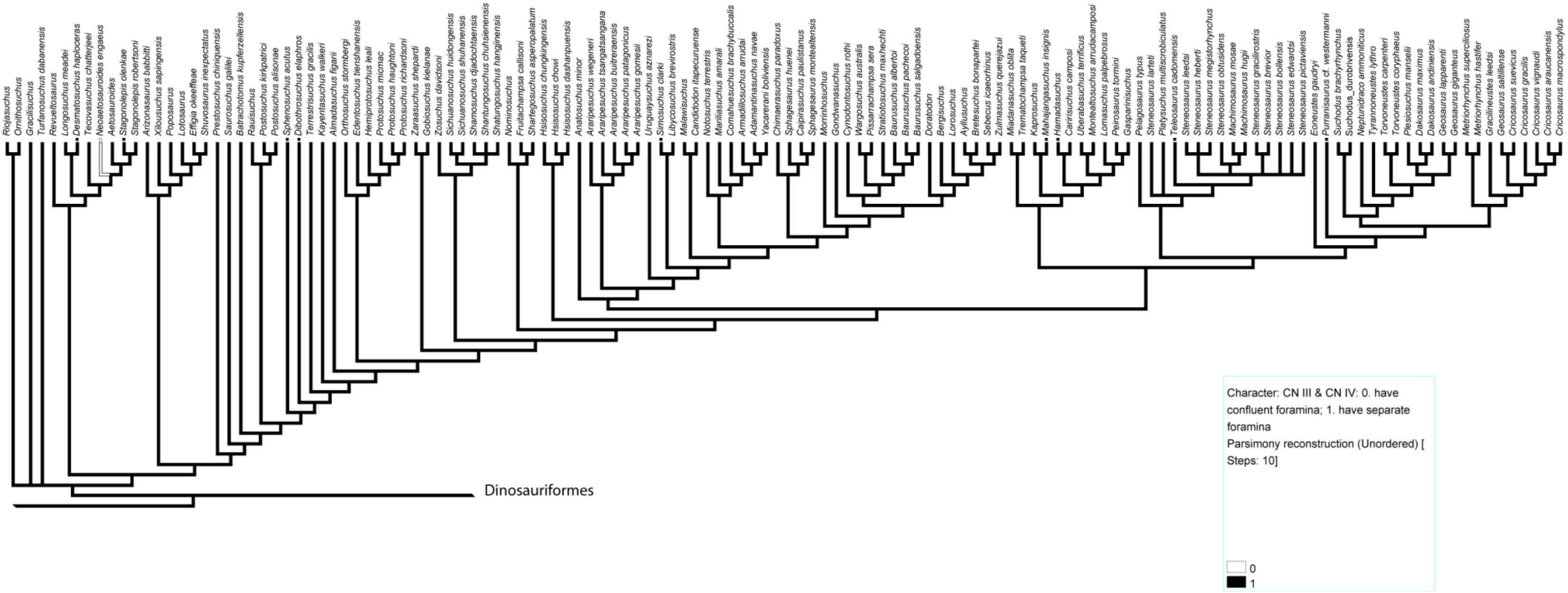

Figure 37: Optimization of character 3 for Pseudosuchia. Please refer to figure for character definition and character states.

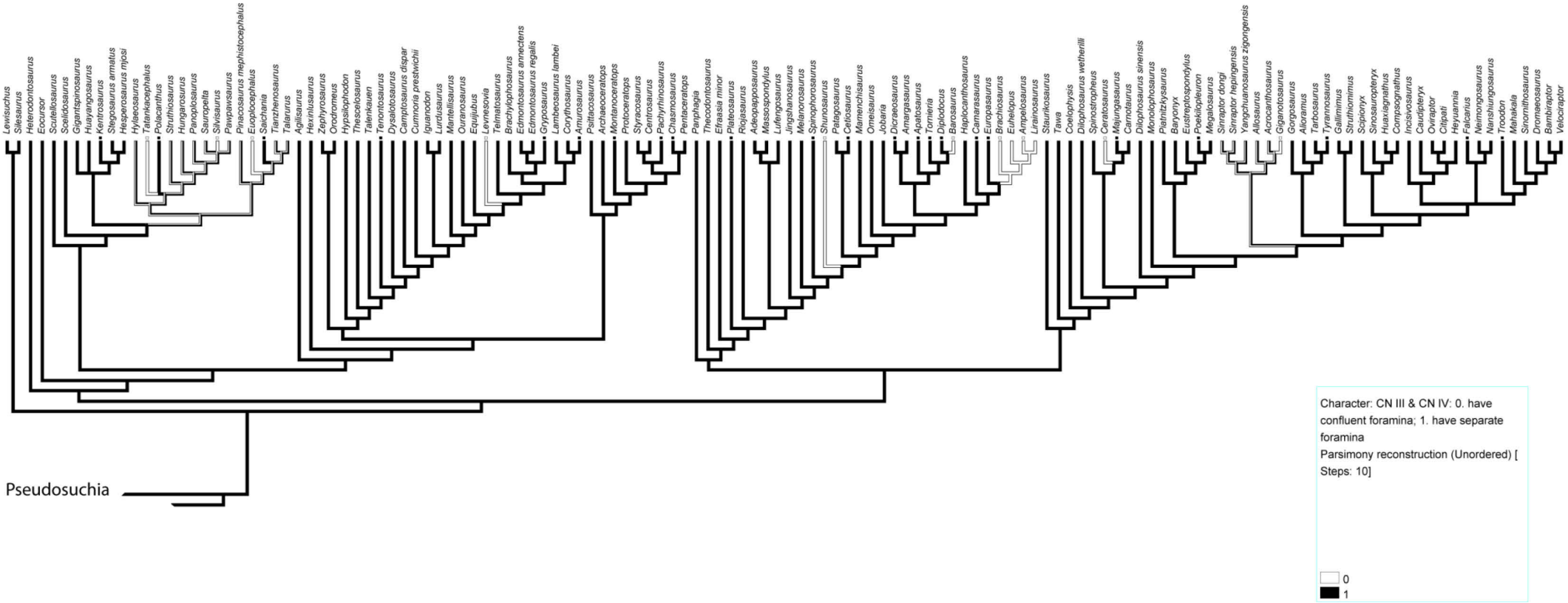

Figure 38: Optimization of character 3 for Dinosauriformes. Please refer to figure for character definition and character states.

movements they can do due to other morphological constraints of the skull. Both avialans and crocodilians show separate foramina for the CN III and CN IV (Baumel 1993, Iordansky 1973).

CHARACTER 4 – ANTERO-POSTERIOR SUB-DIVISION OF THE CN V FORAMEN: ABSENT (0), PARTIAL (1), OR TOTAL (2).

The trigeminal nerve is a composite nerve comprising three different branches: the ophthalmic (V_1), the maxillary (V_2), and the mandibular (V_3). The ophthalmic ramus has a different embryonic origin (placode) from that of the maxilla-mandibular ramus (neural crest), and in anamniotes it usually emerges separately from the brain (Kardong 2001). It is mostly sensory (V_1 and V_2), but also has some motor function in the mixed V_3 branch. It enervates a very diverse group of tissues and muscles that include the regions of the nose, mouth, facial skin, cornea, teeth, palate, and pharynx, among others. It is, therefore, the largest of the cranial nerves. The CN V leaves the braincase anterior to the otic capsule, between the perfacial commissure posteriorly and the pila antotica anteriorly, through the fenestra prootica. The enlarged Gasserian (or trigeminal, semilunar) ganglion is usually positioned outside the brain cavity, where it gives rise to the three branches. Therefore, the lateral braincase wall is pierced by a big foramen for the CN V (prootic foramen, prootic incisure). However, a partial or complete separation between the ophthalmic and maxilla-mandibular branches may occur, as the ganglion becomes progressively more internalized.

Optimization: The ophthalmic and the maxilla-mandibular branches of the CN V diverge external to the brain cavity in most taxa studied (Figure 39, 40). In *Stagonolepis* (LT), however, the branches leave the braincase in separate foramina. Such an anatomy also occurs in *Montanoceratops* and *Pachyrhinosaurus* in the Late Cretaceous (and might be present in Ceratopsia in general, arising then during the Late Jurassic), in *Shunosaurus* (MJ), in Tyrannosauridae (LC), *Falcarius* (EC) and *Troodon* (LC). Therefore, the plesiomorphic condition for Coelurosauria (MJ), Tyrannosauria (LJ), Ornithomimosauria (LC), Compsognathidae (LJ), Therizinosauria (EC), and Deinonychosauria (EC) can be either one or two foramina. An incomplete sub-division of the foramen occurs isolatedly in *Postosuchus alisonae* (LT), *Cetiosaurus* in the Middle Jurassic (and perhaps for Cetiosauridae earlier, in the Early Jurassic), *Dicraeosaurus* in the Late Jurassic (and maybe Dicraeosauridae), *Ampelosaurus* (LC), and *Poekilopleuron* during the Middle Jurassic (and therefore for Megalosauridae earlier in the Late Triassic). *Incisivosaurus* (EC) also has a pinched-off foramen but since *Citipati* (LC) has only one, the condition is unresolved in Oviraptorosauria (EC).

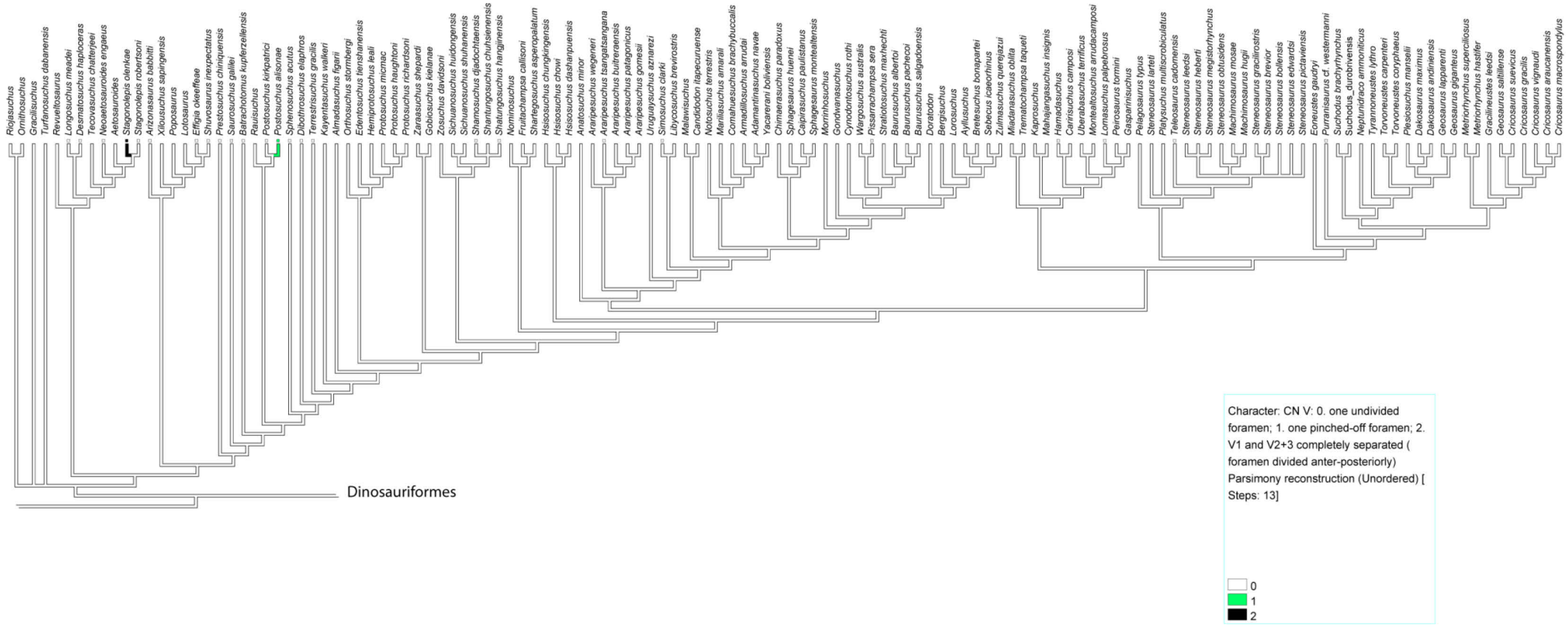

Figure 39: Optimization of character 4 for Pseudosuchia. Please refer to figure for character definition and character states.

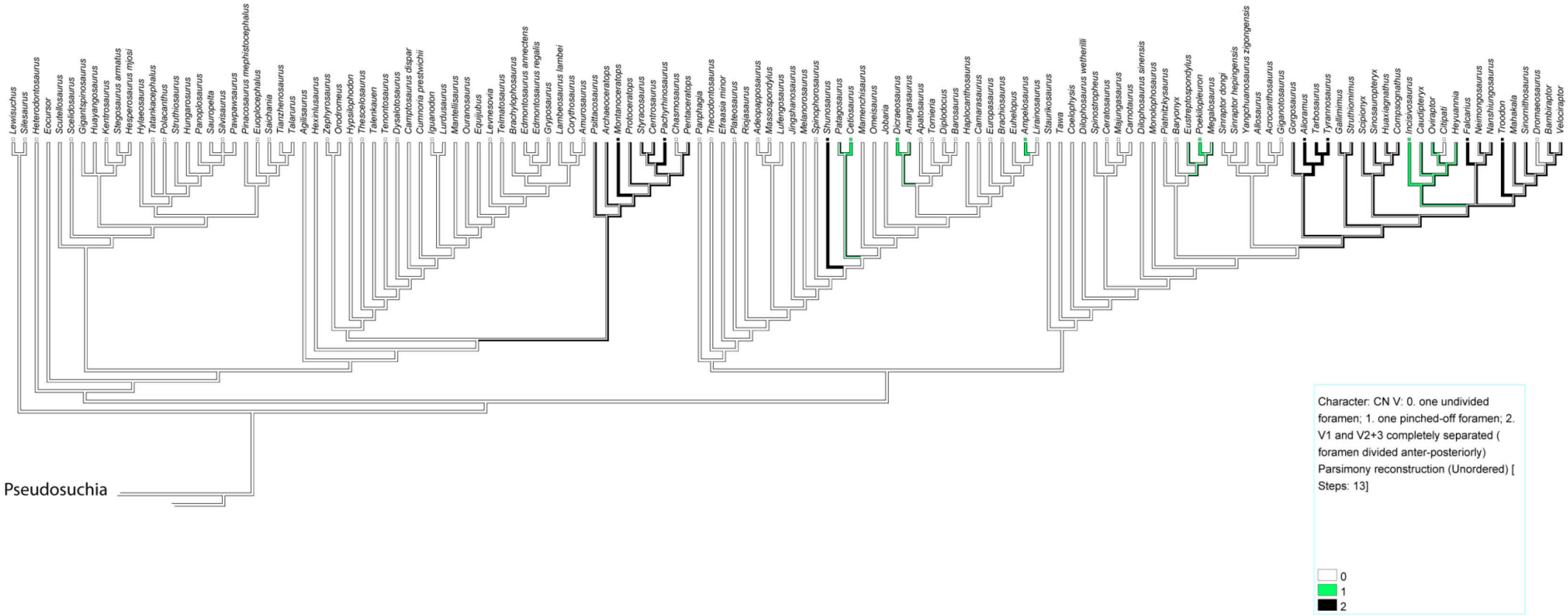

Figure 40: Optimization of character 4 for Dinosauriformes. Please refer to figure for character definition and character states.

Discussion: As in the case of the previously discussed cranial nerves, it is not clear what would be the relationships of single or separate foramina for the role of the trigeminal nerves and its branches. The deeply different morphologies of the avian and crocodilian skulls, however, offer some tempting correlations to be made. The ophthalmic and maxilla-mandibular branches have separate foramina in avialans, but not in crocodilians (Figure 41A). As already mentioned, vision seems to play a very important role in the biology and skull morphology of avialans. Therefore, most of the other facial regions appear secondary, especially those related to the jaw. Avialans are toothless and most have no particularly developed jaw musculature, as functions were transferred to the hind limbs, but still they have separate foramina for the ophthalmic and maxillo-mandibular branches – and in some species even further separations for the maxillary and mandibular rami (Baumel 1993). Crocodilians, on the other hand, have a single foramen for the CN V (Figure 41B). Although it is common in crocodilian literature for ophthalmic and maxilla-mandibular foramina to be mentioned, these refer to extra-cranial divisions, the different foramina being a result of the abutting of the quadrate and pterygoid bone against the braincase, forming the lateral wall of the trigeminal fossa (Holliday & Witmer 2009). However, crocodilians do rely significantly more on mechanisms that are directly innervated by its branches, in particular the adduction of the lower jaw muscles and the "dome pressure receptors" located in their face and mandible, and present also in numerous fossil forms (George & Holliday 2013). However, due to the lack of information on the evolution of most of their sensory systems, it is difficult to postulate if this extra-cranial division was hampered by the very peculiar anatomy of the crocodilian braincase, and whether separate foramina play any role in the development of the nerve.

CHARACTER 5 – COURSE OF THE CN VI: MEDIAL (0), OR LATERAL (1).

The abducens nerve is a motor nerve that also assists in the movements of the eye. It leaves the brain cavity antero-ventrally into the hypophyseal fossa region. As the anterior region of the braincase becomes more ossified, it pierces either the dorsum sellae, or the antero-latero-dorsal part of the basisphenoid. The course of the CN VI may, however, deviate laterally and even not enter the hypophyseal fossa at all. As it is difficult to discern between the latter two cases, into the lateral portion of the hypophyseal fossa or lateral to the hypophyseal fossa as a whole, I decided only to discriminate between a more median route from a more lateral one.

Optimization: The abducens nerve leaving the braincase and entering the hypophyseal fossa is plesiomorphic for Archosauria. The change to a more lateral route, where the CN VI

passes lateral to the hypophyseal fossa, is found only in certain terminal taxa.

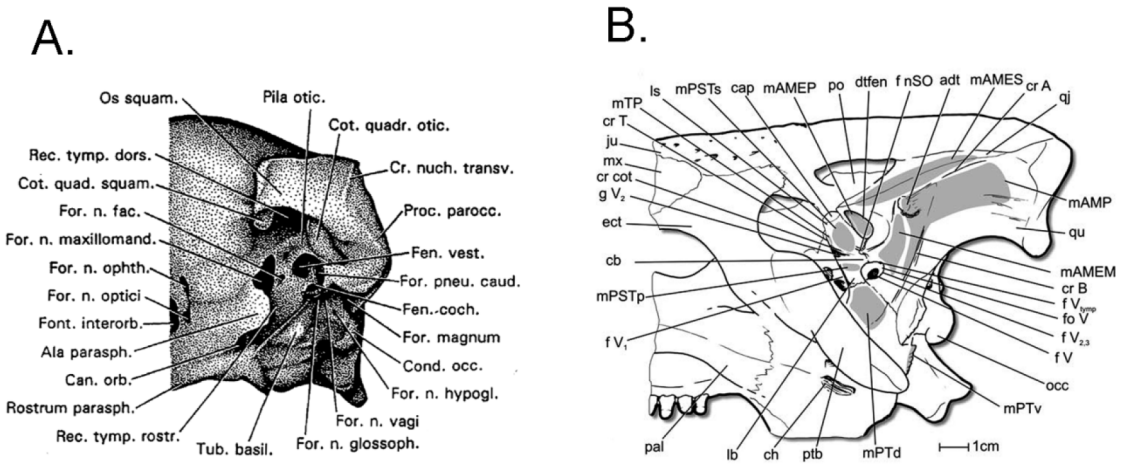

Figure 41: Lateral braincase wall of extant archosaurs. A) *Fregata* – Dinosauriformes (from Baumel 1993); B) *Alligator* – Pseudosuchia (from Holliday & Witmer 2009). dtfen: dorsotemporal fenestra; f V: foramen for the trigeminal nerve; f $V_{2,3}$: foramen for the maxilla-mandibular branch of the trigeminal nerve; f V_{tymp}: foramen for the chorda tymapni branch of V_3; fo V: fossa for the trigeminal nerve; For. n. fac.: facial nerve foramen; For. n. maxillomand.: foramen for the maxilla-mandibular branch; For. n. ophth.: foramen for the ophthalmic branch (V_1) of the trigeminal nerve; For. n. optici: foramen for the optic nerve; g V_2: groove for the maxillary branch of the trigeminal nerve; Rec. tymp. dors.: dorsal tympanic recess; Rec. tymp. rostr.: anterior tympanic recess. For other abbreviations please refer to the original papers.

In Pseudosuchia (Figure 42) it occurs in *Arizonasaurus* during the Middle Triassic (Poposauroidea, MJ), *Postosuchus kirkpatricki* in the Late Triassic (Rauisuchia, LT), *Shantungosuchus* (EC), and *Simosuchus* in the Late Cretaceous (Notosuchia, EJ). For Dinosauria (Figure 43), a change in the course of the CN VI takes place in Ankylosauria (MJ), in *Dicraeosaurus* and *Apatosaurus* (Diplodocoidea) with a reversal in *Diplodocus* during the Late Jurassic, in Titanosauria during the Late Cretaceous (and possibly slightly earlier in Titanosauriformes in the Late Jurassic), and in Avetheropoda in the Late Triassic with a reversal to a more medially-directed route in *Alioramus* in the Late Cretaceous.

D i s c u s s i o n : The hypophysis is a small gland that has a great impact in the physiology of vertebrates, as it is responsible for the secretion of a diverse array of hormones. The deviation of elements away from the hypophyseal fossa could indicate its development as a whole, or of some of its parts, but also the arrangement of the anterior braincase region due to the relative growth of the eyes. The course of the abducens nerve has been discussed very seldomly in the literature. As noticed above, the plesiomorphic state for archosaurs is to have the course of the CN VI medially directed, into the hypophyseal fossa, and in

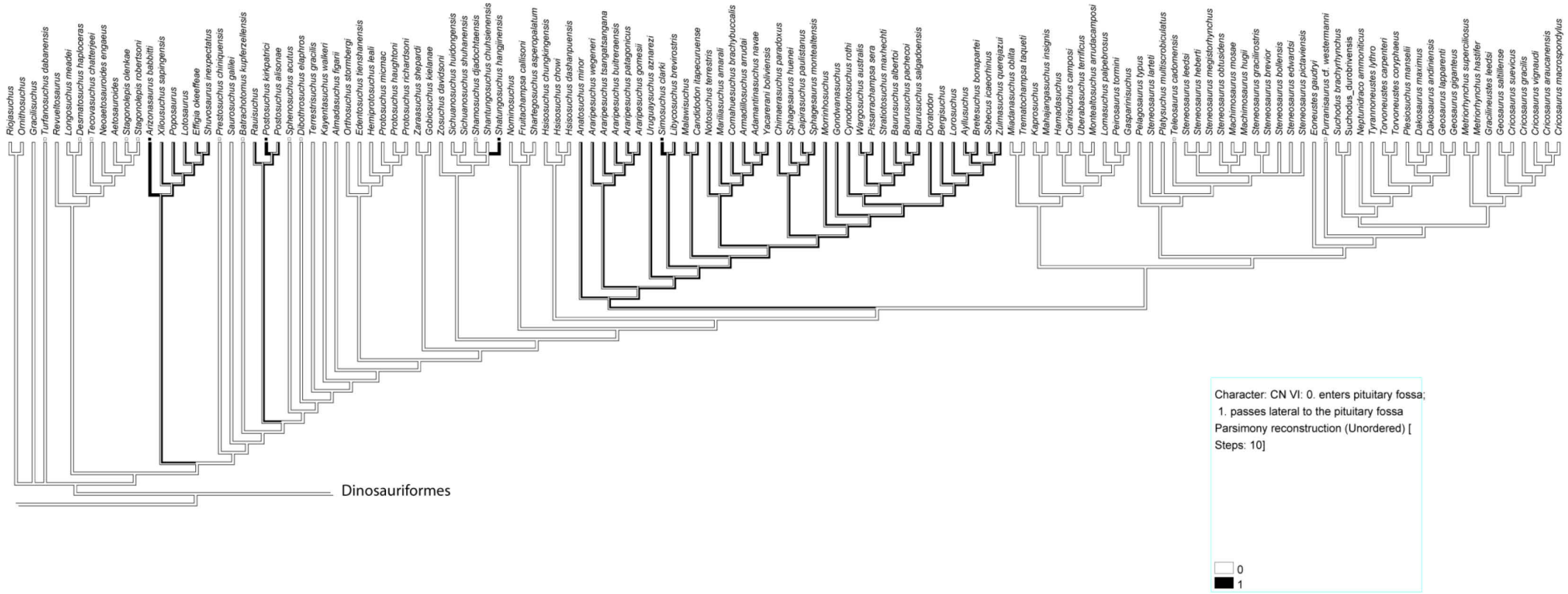

Figure 42: Optimization of character 5 for Pseudosuchia. Please refer to figure for character definition and character states.

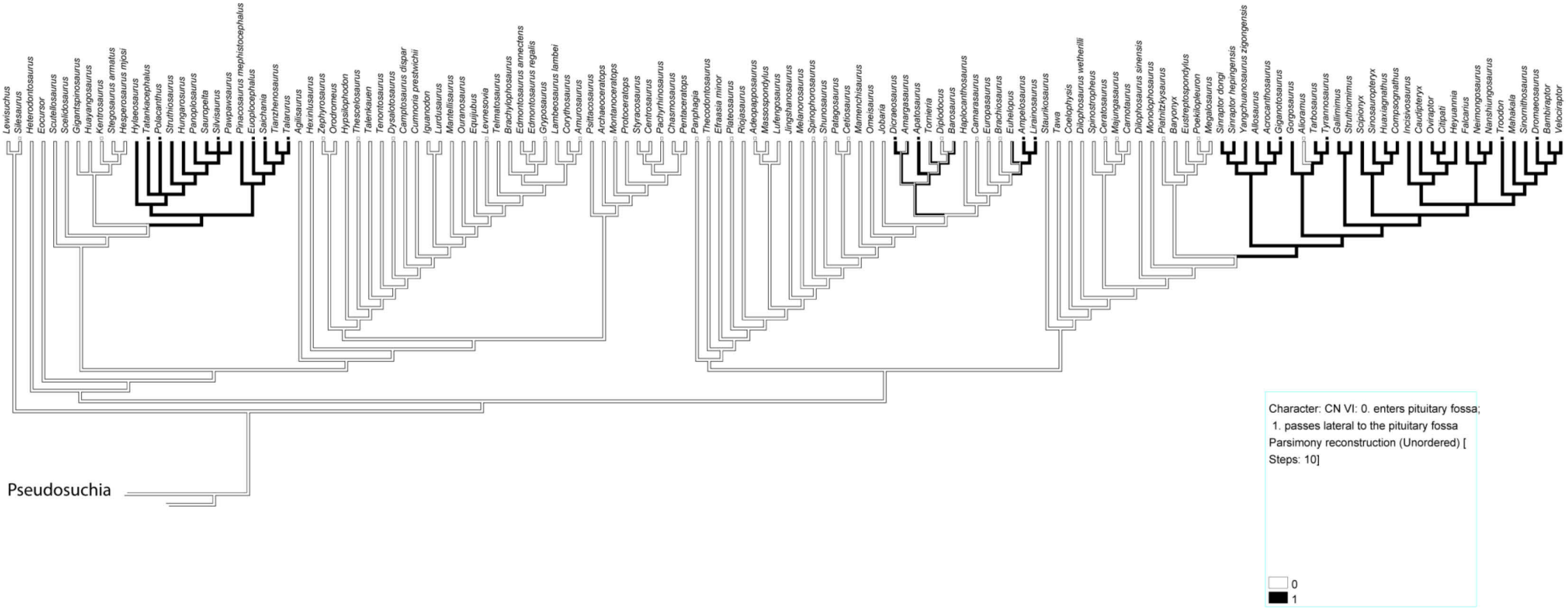

Figure 43: Optimization of character 5 for Dinosauriformes. Please refer to figure for character definition and character states.

crocodilians the plesiomorphic state is retained, with the abducens nerves exiting the braincase into the hypophyseal fossa, although in a more lateral position (Iordansky 1973). A reversal has been noted in *Alioramus*, however (Bever *et al*. 2011). It was suggested in the cited paper that the plesiomorphic state would also be found in non-coelurosaurian theropods and that the morphology in *Alioramus* could represent an intermediate stage in the transition between states. However, with the present findings, corroboration of this hypothesis becomes difficult, as a laterally diverted route was also found in *Giganotosaurus*, implying in its presence for other allosauroids as well. It is, thus, more parsimonious to interpret *Alioramus* as representing a secondary reversal, supporting the other suggested hypothesis. A lateral route for the abducens nerve is found in extant avialans, so it seems that the state change that takes place in Avetheropoda continues without greater changes in the crown-group.

CHARACTER 6 – SUB-DIVISION OF THE CN VII FORAMEN: ABSENT (0), OR PRESENT (1).

The facial nerve is a rather small, mixed nerve which enervates the muscles of the face (motor) and the oral cavity and tongue (sensory). It exits the braincase ventral and slightly anterior to the otic capsule, between the prefacial and the anterior basicapsular, or basicranial, commissures. External to the brain cavity, the CN VII forms a small geniculate ganglion, where it then separates into palatine (VII_{pal}) and hyomandibular (VII_{hym}) branches, where the chorda tympani is a further derivate from the latter. The foramen of the CN VII may become sub-divided antero-posteriorly for each of its branches (Witmer & Ridgely 2009), and the palatine ramus may become more closely associated with the maxillo-mandibular (V_{2+3}) ramus of the trigeminal nerve (CN V).

Optimization: The trigeminal nerve separates into palatine and hyomandibular branches outside of the braincase in most archosaurian taxa (Figure 44, 45). However, the splitting takes place in the brain cavity or in the braincase wall, resulting in separate lateral foramina for each branch only in certain terminal dinosaurian taxa: *Heterodontosaurus* (LT), *Iguanodon* (LJ), *Amurosaurus* (LC), *Shunosaurus* (MJ), and *Alioramus* and *Tyrannosaurus* (and thus Tyrannosauridae, LC). As a consequence, this state might represent the plesiomorphic condition for Iguanodontidae (LJ), Lambeosaurinae (LC), and Tyrannosauroidea (LJ).

Discussion: As confirmed by the mapping of this character, an intra-cranial division of the facial nerve is a rare and punctual event, and its significance remains very speculative. It seems, however, to have some minor confusion in the literature regarding nomenclature.

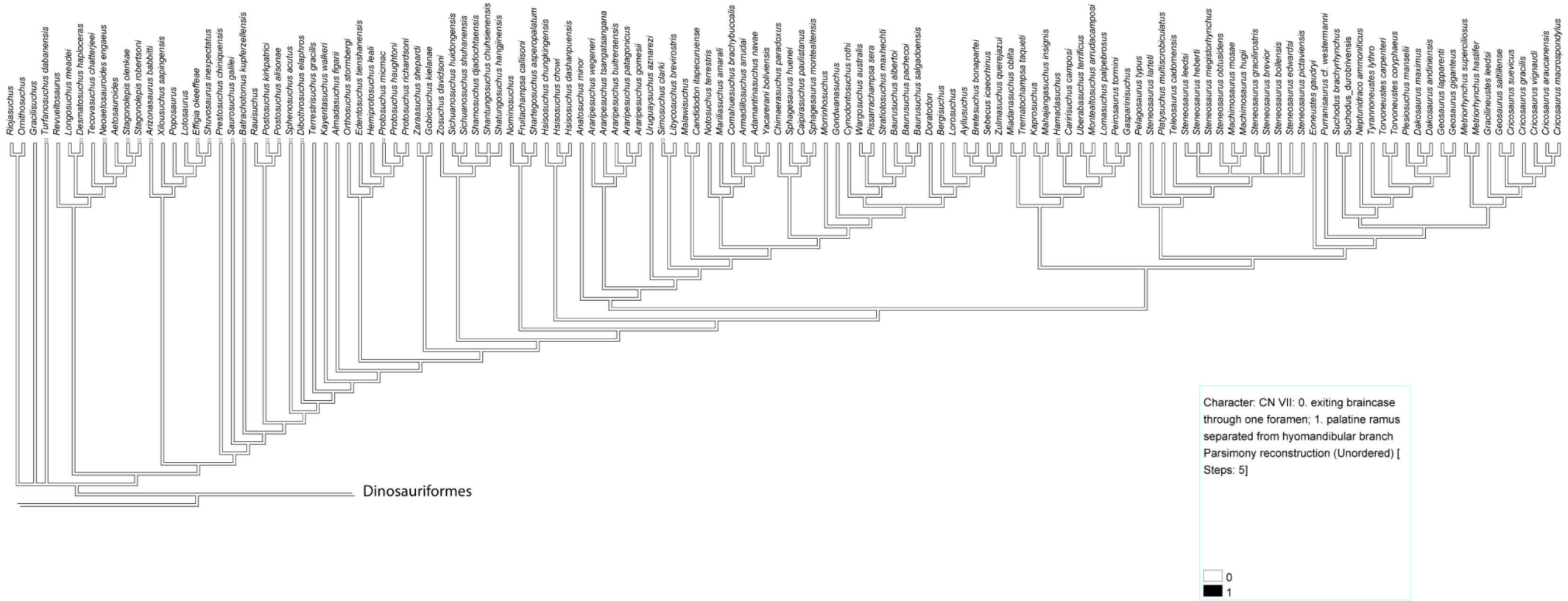

Figure 44: Optimization of character 6 for Pseudosuchia. Please refer to figure for character definition and character states.

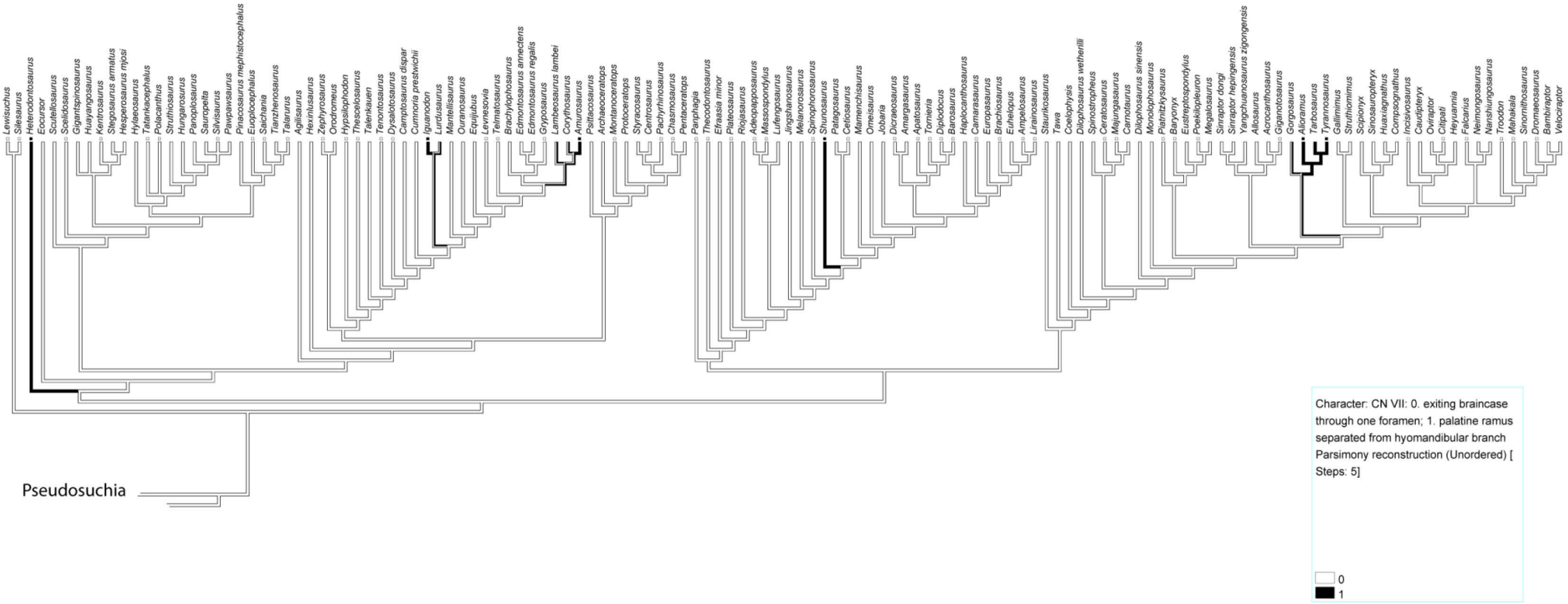

Figure 45: Optimization of character 6 for Dinosauriformes. Please refer to figure for character definition and character states.

One potential explanation for this may be the course of the palatine branch and the fact that in earlier times, the identification of structures was more influenced by mammalian and human nomenclature than it currently is. After branching off, the palatine branch of the facial nerve extends ventrally onto the basisphenoid and then into the vidian groove or canal. Thus, this ramus was also called “vidian nerve” whereas the facial foramen was often termed chorda tympani foramen, in reference to the more well-known of the other facial ramifications. Because these structures are relatively far from each other, and because the vidian canal is an important structure carrying other elements such as the internal carotid artery, this misunderstanding of terms does not seem that widespread, although several such examples can be found in the literature. For instance, when describing the braincase of the *Euparkeria* specimen SAM-PK-5876, Ewer (1965) identified two separate openings for the palatine and the “chorda tympani” branches of the facial nerve. Cruickshank (1970) and Welman (1995) also identified two foramina for the specimen SAM-PK-7696, although Evans (1986) identified one opening, but erroneously discarded the dorsal foramen and chose a structure that bears no relationships to any foramen instead. Our approach confirms the identification of Gower & Weber (1998) for UMZC T692 and the processing of the scans of the holotype will likely confirm this pattern for *Euparkeria*. Furthermore, given the small size of the facial foramen, it becomes easily obliterated by sediment, and appears as if it was not preserved when the braincase suffers even the slightest deformation. Therefore, it is not surprising that Evans (1986) did not find a facial foramen for the *Prolacerta* specimens under study. However, the statement that “[t]he existence of an enclosed facial foramen depends on the degree of ossification of the lateral braincase wall” (Evans 1986:196) seems puzzling. The position of the foramen of the CN VII near the otic capsule makes it enclosed by bone even when the degree of ossification of the prootic is very modest and basically restricted to its posterior portion and to the paroccipital process, as in *Captorhinus* (Heaton 1979).

For *Shunosaurus*, the identification was difficult. Figure 7 of Chatterjee & Zheng (2002) shows only one foramen for the facial nerve, but the text reports two foramina. The dorsal one would be for the hyomandibular branch and the ventral one for the “ramus communicans branch of the facialis”, likely referring to the communication of the palatine ramus with the vagal complex (Willard 1915 – see below). The identification of two foramina for *Heterodontosaurus* was based on figure 15 of Norman *et al*. (2011), where the lateral braincase wall is depicted with some unidentified structures. Only one foramen for the facial nerve is labelled, but the presence of what seems to be another, very closely related foramen just ventral to the former is intriguing. By the figure it is more similar to a foramen, but by the text this actually seems to represent a recess, which was identified as the auditory recess. In either case, this is a misidentification. When present, the auditory recess is a structure that

indeed contains the facial nerve foramen, but it is located on the medial side of the lateral braincase wall, not on the lateral (Oelrich 1956, Sobral *et al*. 2012).

CHARACTER 7 – FENESTRA PSEUDOROTUNDA: ABSENT (0), OR PRESENT (1).

This character has the simple objective of differentiating the presence of a metotic foramen to the apprearance of a fenestra pseudorotunda and a vagus foramen. As the sub-division of the metotic foramen is the key character investigated in this study, the different anatomies and processes underlying it should be clear at this point and need no further explanation. However, a little can be added on the function and morphology of other associated elements that were described in less detail.

The glossopharyngeal nerve (CN IX) has sensory branches carrying information from the pharynx and the tongue and innervates muscles of the third branchial arch (Kardong 2001). It leaves the braincase through the metotic foramen, together with the vagus and accessory nerves, but when the fenestra pseudorotunda is present it can show a variable course out of the brain cavity. In lizards, when the metotic foramen becomes subdivided, the CN IX usually has an extra-capsular course, leaving the braincase through the medial and lateral openings of the recessus scalae tympani (i.e., though the apertura medialis and through the fenestra pseudorotunda). However, it can also pierce the otic capsule medially at the cochlear recess (internal glossopharyngeal foramen), pass into the recessus scalae tympani through the perilymphatic foramen (or through another foramen or canal in the crista interfenestralis – the former being very common in turtles) and leave laterally through the fenestra pseudorotunda or through its own foramen anterior to the latter (Bellairs & Kamal 1981). It can also have an extra-capsular course, but with its own medial or lateral foramen (Rieppel 1978). In crocodilians, the CN IX leaves the brain cavity through the vagus foramen, but it avialans it may alternatively pass through the fenestra peudorotunda (Rieppel 1985). Thus, given the highly variable course of the CN IX out of the brain cavity, it is not a good landmark for identification of braincase structures.

The glossopharyngeal nerve has an important communication with the facial, which deserves some brief attention because of the description of Iordansky (1979) on the anatomy of crocodilians. Once it leaves the brain cavity, the CN IX crosses the middle ear cavity on its medial wall into the proximal neck area where a group of its fibers communicates with one of the cervical sympathetic trunks and then immediately joins the palatine branch of the CN VII to innervate the palate (Oelrich 1956). The sympathetic trunk is the main component of the sympathetic division of the autonomous nervous system. It consists of a pair of nerve fibers running parallel to the vertebral column that connect to the spinal nerves through the paravertebral ganglia (Kardong 2001). Some authors refer to the communication between the glossopharyngeal nerve and the cervical sympathetic trunk as Jacobson's Anastomosis

(Oelrich 1956), while others use this term for the joining of the CN IX with the palatine branch of the CN VII (Willard 1915). Small connections between nerves are called generally ramus communicans, and thus this communication has also been termed “ramus communicans internus rami palatini cum glossopharyngeo” (Willard 1915:81). In the description given by Iordansky (1973:226), the big vagus foramen is sub-divided internally in two different canals. The medial one extends to the brain cavity and would thus be the vagus foramen *sensu*, *stricto* while the lateral canal extends to the middle ear cavity and would carry the “Ramus communicans (N. sympathicus) connecting the VIIth and IXth nerves”. This canal was identified by Witmer *et al*. (2008:73) as the “canal for the tympanic branch of the glossopharyngeal (CN IX) and vagus (CN X) nerves” – which would communicate with the poorly known tympanic branch of CN V. As mentioned throughout this text, the anatomy of crocodilians is incredibly understudied, and the existence of this small trigeminal branch and its connection with both glossopharyngeal and/or vagal nerves seems to only have been noted twice in the literature (Holliday & Witmer 2009:717), and indeed is not mentioned in other reptilian references. Although the anatomical details of these connections may, at the moment, not be vital in a palaeontological context for the identifications of the structures, a clarification of the terms used by Iordansky (1973), but yet not widespread in the literature seemed appropriate.

The vagus nerve (CN X) is an important nerve composed of several small roots that have both sensory and motor functions. It has a widely distributed range of action, innervating a series of tissues in the mouth, pharynx, larynx, the heart and many other visceral elements (Kardong 2001, Oelrich 1956). It leaves the braincase throught the metotic foramen or, when it becomes sub-divided by the metotic strut, by the vagus foramen, located posterior to the fenestra pseudorotunda. As usual, the vagus has several communications with other cranial nerves, in particular the glossopharyngeal and hypoglossal nerves. Finally, the accessory nerve (CN XI) is a small nerve whose composition is rather confusing. It is traditionally described as being composed of cranial and spinal parts, but as the cranial part soon becomes associated with or is formed by the posterior extension of some of the roots of the vago-glossopharyngeal complex, usually only its spinal part is considered, which has, in turn, contributions of the 2nd and 3rd spinal nerves (Oelrich 1956, Wilard 1915). It is absent in many squamates, but in avialans and mammals it is very distinct (Kardong 2001). It enervates muscles of the shoulder girdle and has no foramen of its own, and always leaves the braincase, when present, with the vagus nerve.

Optimization: The sub-division of the metotic foramen does not represent a plesiomorphy for Archosauria. In Pseudosuchia (Figure 46), the fenestra pseudorotunda appears in Crocodylomorpha in the Late Triassic before the branching off of *Almadasuchus*,

and possibly slightly earlier. The sub-division of the metotic foramen also represents the plesiomorphic condition for Ornithischia in the Middle Triassic (Figure 47), but reversals occur in Eurypoda (EJ), *Hypsilophodon* (EC), *Telmatosaurus* (LC), and in *Chasmosaurus* (LC), the latter perhaps representing a reversal in Chasmosaurinae. During the Early Cretaceous, the fenestra pseudorotunda appears again in *Silvisaurus*, *Pawpawsaurus*, *Sauropelta* and possibly *Panoplosaurus*. In Sauropodomorpha, the fenestra pseudorotunda appears in some isolated taxa only, such as *Cetiosaurus* in the Middle Jurassic (and maybe earlier in Cetiosauridae, in the Early Jurassic) and in *Barosaurus* (LJ). The fenestra pseudorotunda did not appear early in the phylogenetic history of Theropoda. A sub-division of the metotic foramen takes place in *Majungasaurus* in the Late Cretaceous (or perhaps earlier in Abelisauridae in the Late Jurassic), in *Poekilopleuron* (MJ) and *Baryonyx* (EC), possibly representing the plesiomorphic state for Megalosauria in general in the Late Triassic, and in Coelurosauria also in the Late Triassic. In the latter case, there is a reversal in Oviraptorosauria during the Early Cretaceous.

D i s c u s s i o n : The scoring of this character was very difficult for later pseudosuchians, given the very peculiar morphology of their otic region. Walker (1990) described an undivided metotic foramen for *Sphenosuchus*, but argued for the presence of a fenestra pseudorotunda in this taxon, as noted by Gower & Weber (1998) and Gower & Walker (2002), and followed by Wu & Chatterjee (1993) for *Dibothrosuchus*. Their intricate otic morphology and the attempts to homologize terms are in part responsible for the complexity of the matter. Although the otic morphology of crocodilians has been briefly described previously, it is now appropriate to enter some more subtle level of detail in a more evolutionary context.

In avialans, the ventral ramus of the opisthotic extends anteroventrally, and its distalmost tip is expanded at the contact with the prootic (Figure 10A). Thus, the fenestra pseudorotunda is framed by the opisthotic antero-dorsally and by the exoccipital postero-ventrally. The overall otic region of extant archosaurs is rotated dorsally, so that the fenestra ovalis lies antero-dorsally to the postero-ventral fenestra pseudorotunda. In crocodilians, the ventral ramus of the opisthotic is developed so that it bends sharply postero-ventrally at about the antero-dorsal corner of the fenstra pseudorotunda, and then again dorsally and slightly medially on its ventral rim (Figure 9E). In both groups of extant archosaurs, the medial braincase wall is ossified as the opisthotic extends ventrally, but in crocodylians, this extension also takes place laterally. Therefore, the bending of the ventral ramus makes the opisthotic contact itself, excluding the exoccipital from the border of the fenestra pseudorotunda (Gower & Walker 2002, Gower & Weber 1998). This is an intricate

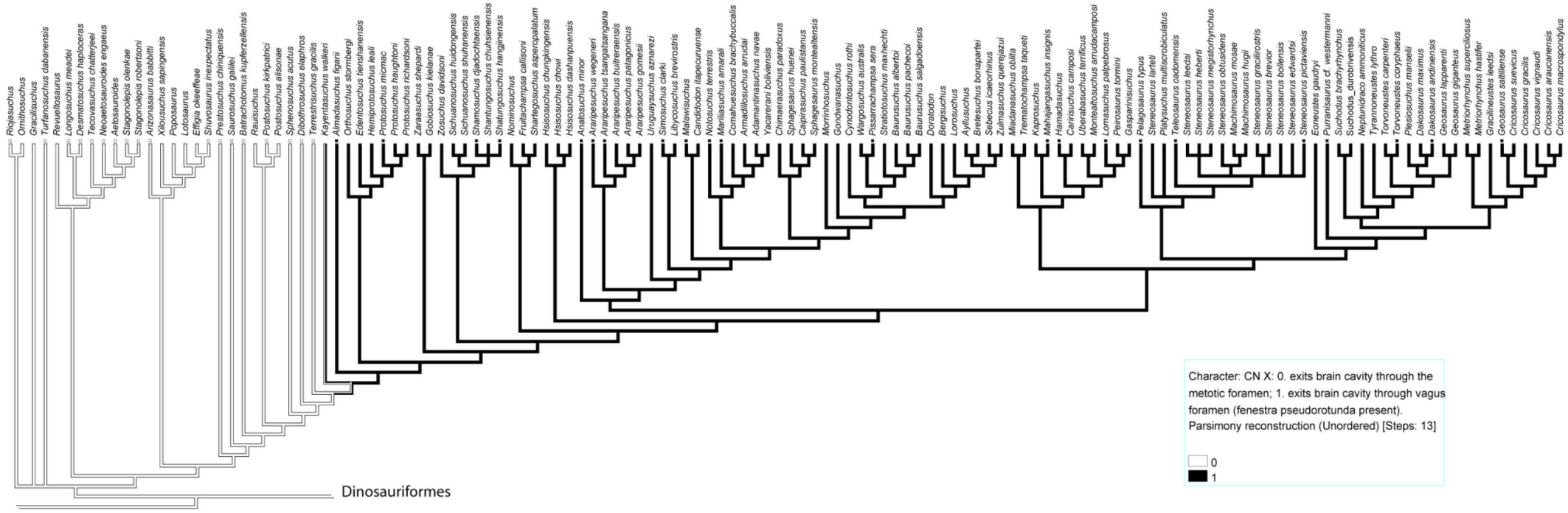

Figure 46: Optimization of character 7 for Pseudosuchia. Please refer to figure for character definition and character states.

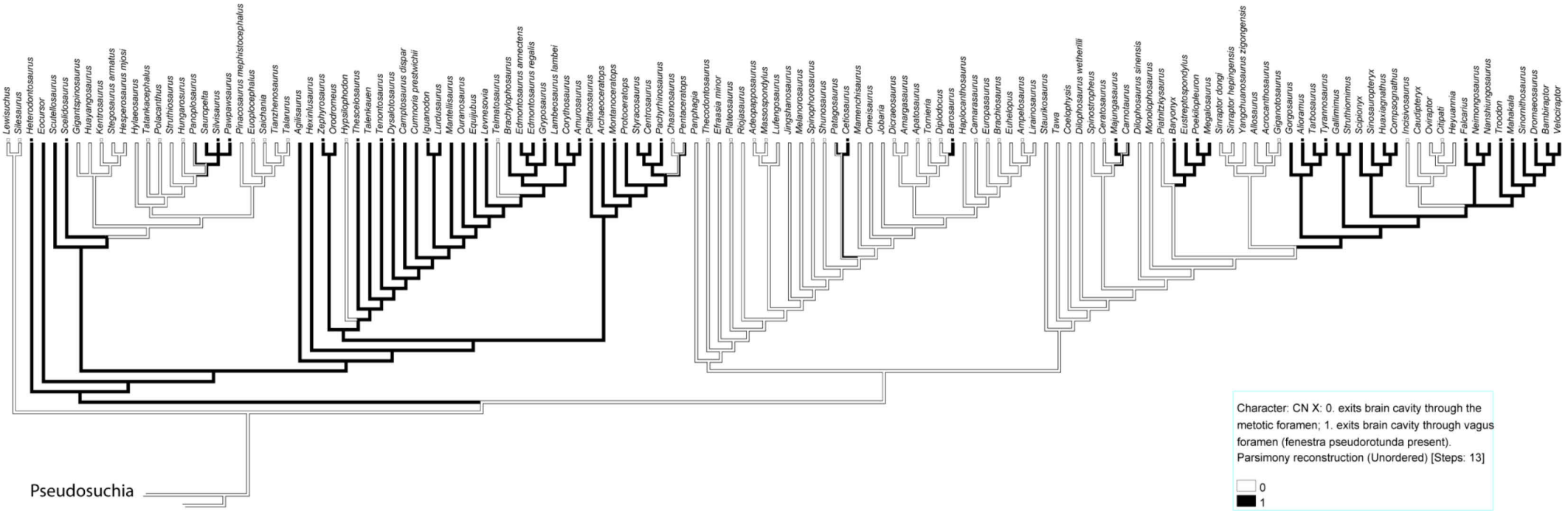

Figure 47: Optimization of character 7 for Dinosauriformes. Please refer to figure for character definition and character states.

morphology that seems to have started evolving very early on the pseudosuchian side of the archosaurian tree only, and the completion of this “opisthotic loop” is already present in *Sphenosuchus* (Walker 1990).

The otic region of later archosauriforms such as *Erythosuchus* (Gower 2002, Gower & Sennikov 1996, and pers. obs. of materials in English and South African collections – see Table 1) is very similar to that of *Euparkeria*: the ventral ramus of the opisthotic extends ventrally in a very vertical manner to contact the basisphenoid and the basioccipital, separating the undivided metotic foramen from the anteriorly located fenestra ovalis. Gower & Walker (2002) argued for a closer phylogenetic relationship between aetosaurs and crocodylomorphs, and suggested the morphology of *Stagonolepis* would be intermediate between that of non-crown group archosauriforms and *Sphenosuchus*. In it, the shifting of the otic region is present, so that the ventral ramus is inclined from a postero-dorsal to an antero-ventral way. Furthermore, its distal tip is developed and shows a bend on the antero-dorsal corner of the metotic foramen, where it then extends ventrally to contact the prominent lateral ridge of the exoccipital on the posterior border of the metotic foramen (Figure 48). The assumption that this morphology represented an intermediate step in the otic evolution of pseudosuchians was also based on the presumed more basal position of *Stagonolepis* within Aetosauria. However, with recent reassessment of aetosaurian intra-relationships, it is now considered a rather derived taxon within the group (Roberto-da-Silva *et al*. 2014). The hypothesis defended by Gower & Walker (2002), however, presents an obstacle for the understanding of braincase evolution in aetosaurs. Due to lack of good descriptions and/or illustrations, it is presently unclear what the otic region of basal taxa looked like, but the anatomies of the ventral ramus in more derived taxa such as *Typothorax* (Martz 2002) and *Desmatosuchus* (Small 2002), despite showing an antero-ventral inclination, seem to largely conform to non-crown group archosauriforms in having no distal bend (Figure 49A, B) – or, at least, not as strong a bent ramus as reported by Gower & Walker (2002). This also seems to be the case for closely related taxa such as *Stagonolepis olenkae* (Sulej 2010) and *Calyptosuchus* (pers. obs. of a cast of PEFO 34616, made available to me during a collection visit to the Instituto Miguel Lillo – Figure 49C, D). On the other hand, Gower & Weber (2002) were very careful when describing the braincase of *Stagonolepis*, and it may be that this feature was either overlooked by other authors or not well preserved in the referred specimens. In either case, the otic region of pseudosuchians seems not to have changed drastically until prior to Crocodylomorpha. In a number of taxa, the exact morphology is obscure, but the ventral ramus of the opisthotic of *Prestosuchus* seems to conform to the proposed basal aetosaurian morphology (Mastrantonio *et al*. 2013), whereas the ventral ramus of *Saurosuchus* conforms more closely to non-crown group archosauriforms (Alcober *et al*. 2000 and pers. obs. of PVSJ 32).

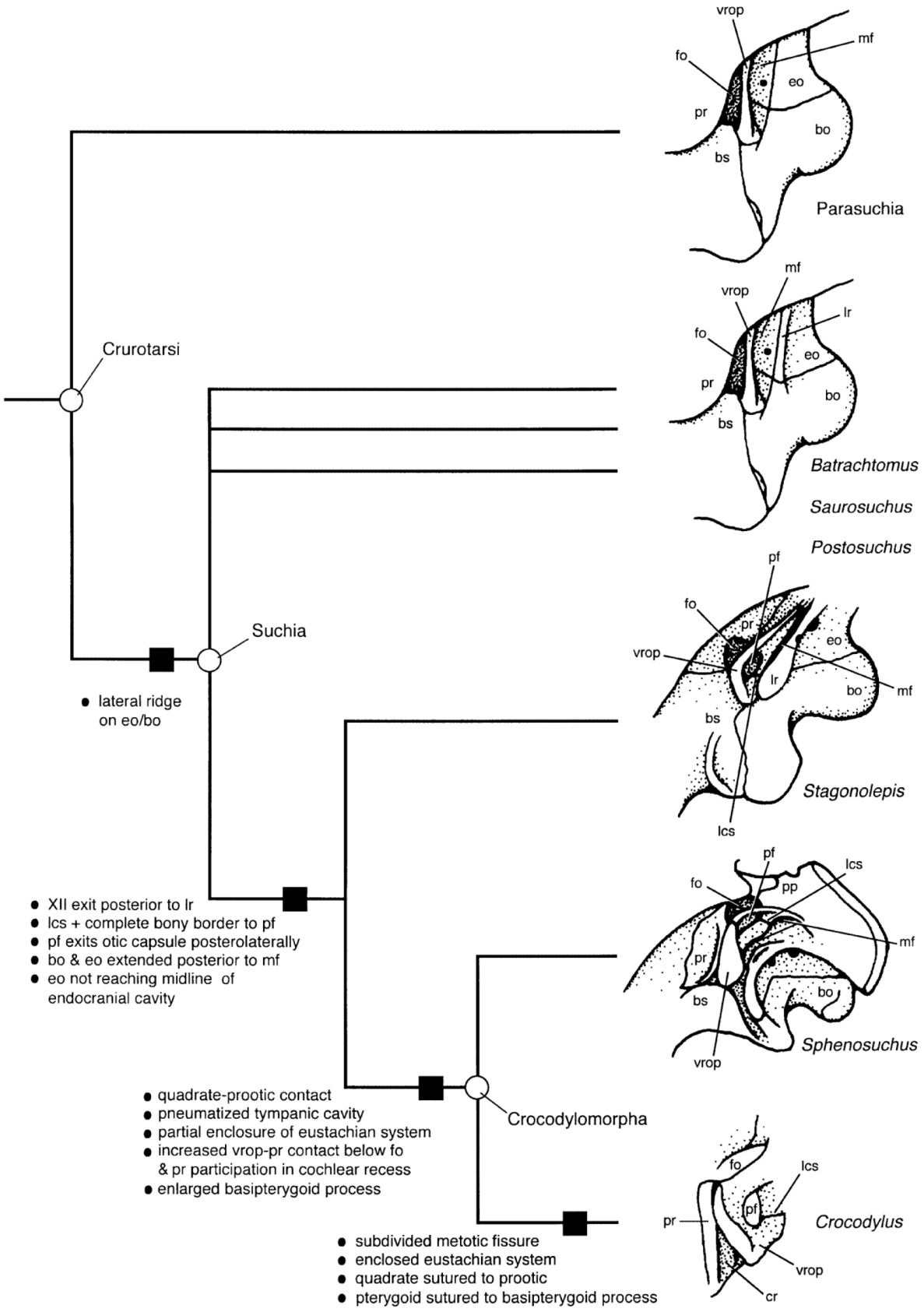

Figure 48: Pseudosuchian braincase evolution. Proposed braincase synapomorphies are shown on some branches. For *Crocodylus*, only the detail of the ventral ramus of the opisthotic is shown. bs: basisphenoid;

The morphology of this area of the braincase in early crocodylomorph taxa such as *Sphenosuchus* and *Dibothrosuchus* is incredibly modified in comparison to closely related clades, and thus it is not surprising that the description of Walker (1990) is very complex. However, the failed attempts of homologizing structures (such as the subcapsular process of crocodilian embryos with the lateral ridge of the exoccipital) complicate it even further. In extant crododylians, the perilymphatic foramen does not connect the cochlear recess to the recessus scalae tympani in a posteriorly or postero-medially directed manner, as is plesiomorphic for archosaurs. Instead, it is rotated laterally, so that it is at least partially visible in lateral view. Therefore, in *Sphenosuchus*, two "foramina" can be seen inside the metotic foramen: the perilymphatic foramen and the metotic "canal". Walker (1990) names the metotic foramen as fenestra pseudorotunda (the lateral opening framed by the opisthotic loop) and the canal of the metotic foramen as metotic foramen itself. Therefore, in his identifications, *Sphenosuchus* possesses both a fenestra pseudorotunda and a (undivided) metotic foramen. And so does *Dibothrosuchus* (Wu & Chatterjee 1993). In *Terrestrisuchus*, the same morphology is found, although Crush (1984) identifies the metotic foramen as being the perilymphatic duct – making these structures completely anatomically inconsistent. These three taxa, therefore, were scored as having no fenestra pseudorotunda.

The sister taxon of Crocodyliformes, *Almadasuchus*, possesses a braincase in many regards very similar to extant taxa, in which, in addition to the appearance of the fenestra pseudorotunda and the secondary tympanic membrane, the paroccipital process is highly developed and ventrally extended, closing off the middle ear cavity posteriorly, with the vagus foramen leaving the braincase through the occipital wall (Pol *et al*. 2013). The lateral braincase wall is not accessible in this taxon, but the occipital region is well preserved, and a vagus foramen was identified, implying in the presence of a fenestra pseudorotunda. The lateral braincase wall can be seen in the early crocodyliforms *Protosuchus micmac* (Sues *et al*. 1996) and *P. haughtoni* (Busbey & Gow 1984). They also possess a vertical and ventrally expanded proccipital process and a vagus foramen located lateral to the foramen of the CN XII, on the occipital surface. This trend persists in all other evaluated crocodyliform taxa, and therefore they were scored as having a sub-divided metotic foramen. It is worth noticing that, in addition to a "metotic foramen" (= fenestra pseudorotunda), the nomenclature in these taxa often includes a "metotic fissure", which is used for the medial entrance of CN IX-XI in the lateral braincase wall.

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bo: basioccpital; cr: cochlear recess; eo: exoccipital; fo: fenestra ovalis; lcs = loop closure suture of ventral ramus of the opisthotic; lr: lateral ridge of the exoccipital; mf: metotic foramen; pf: perilymphatic foramen; pp. paroccipital process; pr: prootic; vrop: ventral ramus of the opisthotic. Foramina for the CN XII are indicated by solid black dots. From Gower & Walker 2002. Refer to original paper for further details.

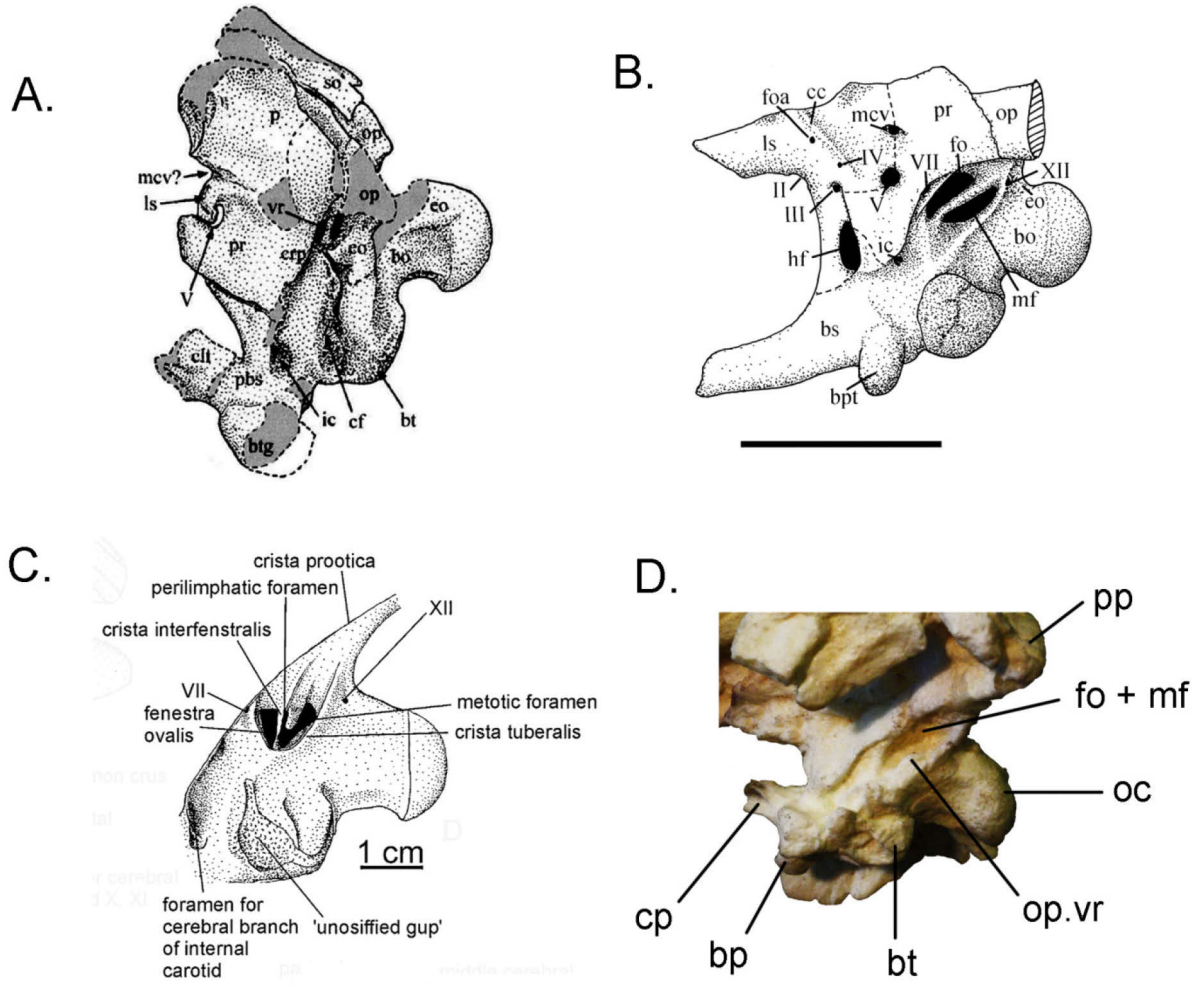

Figure 49: Braincases of aetosaurs in left lateral view. A) *Typothorax* from Martz 2002; B) *Desmatosuchus* from Small 2002; C) *Stagonolepis* from Sulej 2010; D) *Calyptosuchus* (PEFO 34616). bo: basioccpital; bt: basal tuber; btg: basipterygoid process; bp: basipterygoid process; bpt: basipterygoid process; bs: basisphenoid; cc: cotylar crest; cf: crescentic facet; clt: cultriform process; cp: cultriform process; crp: crista prootica; eo: exoccpital; fo: fenestra ovalis; foa: foramen for the ophthalmic artery; hf: hypophyseal fossa; ic: internal carotid foramen; ls: laterosphenoid; mcv: middle cerebral vein; mf: metotic foramen; oc: occipital condyle; op: opisthotic; p: parietal; pbs: parabasisphenoid; pp: paroccipital process; pr: prootic; so: supraoccipital; vr: ventral ramus. Roman numerals: corresponding cranial nerves.

As reconstructed by the analysis and highlighted above, the changes in the otic region of pseudosuchians began very early in their evolutionary history, but happened gradually in the main line without much plasticity. Although the anatomy of the crocodyliform braincase is often inaccessible and its analysis depends largely on exceptional specimens or the application of CT scanning techniques, there is a strong indication that impedance-matching hearing evolved only once in the group, slightly prior to the origin of Crocodyliformes. As briefly explored in the introduction, braincase morphology in the group is very peculiar. The abutting of both the quadrate and pterygoid bones against the braincase wall caused a profound reorganization of braincase structures, including cranial nerves, jaw

adductor musculature, the epipterygoid bone, and the otic region (Holliday & Witmer 2009). These changes are responsible for the akinetic nature of the skull, with tight integration of the palate, braincase, and temporal regions (Pol *et al*. 2013). The fenestra pseudorotunda appears early in this evolutionary sequence, being concomitant with the first modifications towards cranial akinesis such as the basisphenoid-quadrate suture. Although these chacracters were not acquired in a straight sequence, having arisen independently in many different crocodylomorph groups, the selective pressures acting on feeding mechanisms are the main driving force behind the observed anatomical pattern – and which seem to have been strong enough on the otic and occipital regions to allow very little morphological plasticity. The changes imposed on the middle ear of crocodiliforms are then one additional example of parallelism in the evolutionary history of mammals and crocodilians.

In dinosaurian taxa, however, this character is much more variable. The fenestra pseudorotunda occurs several times independently – in my analysis, seven. While it appears very early in ornithischians, in saurischians it occurs only in the origin of Coelurosauria and only in certain terminal sauropodomorph taxa. Among ornithischians, ankylosaurs and hadrosaurs show a trend in increasing elongation and morphological complexity of the airways. While these features are most likely related to thermo- and osmoregulation, a role in vocalisation has also been suggested (Evans *et al*. 2009, Miyashita *et al*. 2011, Witmer & Ridgely 2008b). The lengthening and looping of passages during nasal roaring would result in low frequency calls, a pattern also seen in some mammals and avialans. The absence of the fenestra pseudorotunda would be optimal for the detection of such sounds, but there is currently no indication that the groups mentioned above have lost the fenestra, though it is tempting to make such a link for ankylosaurs. The fact that the reversal occurs early in eurypod history and that stegosaurids show no fenestra, but also no particularly elongate or elaborate nasal passages, reinforce the hypothesis that these two features are likely uncorrelated. Also, other anatomical characters such as the length of the basilar papilla are more closely related to the detection of low frequency sounds (Gleich *et al*. 2005). Because the length of the basilar papilla is directly correlated to body mass, the same analogy could be suggested for saurischians. In Sauropodomorpha, an extreme increase in body size could have presented an extra selective force for the non-development of a fenestra pseudorotunda, but the same argument would not explain why it did appear in large bodied theropods – unless these changes took place in basal, small-bodied members of abelisaurids, megalosaurians and coelurosaurians, and were not lost with increase in body mass By contrast, small oviraptorosaurians show no fenestra pseudorotunda.

A superficial correlation between the aforementioned characters may nonetheless exist, although it is very difficult to test with the data presently available; i.e., in ankylosaurs, the elongation of the airways may represent an extra factor for mantaining of the

plesiomorphic state, while in hadrosaurians other advantages of possessing an impedance-matching mechanism surpassed the need for detection of low frequency sounds. Likewise, the greatly exaggerated body size of sauropods could have been responsible for allometric modifications of inner ear structures that rendered a fenestra pseudorotunda unnecessary, while in theropods other selective forces favoured it and, on the one hand, the subsequent increase in body size in some groups had only a minor influence in this particular character and, on the other, oviraptorosaurians have their own, distinctive evolutionary history regading it. The key would then be finding out why the fenestra pseudorotunda was lost in the first place in eurypods and why it has been developed in Coelurosauria. In any case, independent of the explanation for each group in particular, the reconstruction of the ancestral state of this character is another example of the morphological plasticity allowed in dinosaur braincases in contrast to that seen in pseudosuchians. It also gives further evidence for the idea that many anatomical characters of extant avialans were already present in more basal clades of theropod dinosaurs.

CHARACTER 8 – NUMBER OF CN XII FORAMINA: ONE (0), OR TWO OR MORE (1).

The hypoglossal nerve (CN XII) is a motor nerve primarily innervating the mucles of the tongue and the hyoid apparatus. As the occipital and pre-occipital arches of the embryo are postulated to be homologs of the vertebral column elements (Evans 2008), the posterior nerves of the cranial series bear many similarities with spinal nerves, in particular the CN XII. In squamates, the hypoglossal nerve has three roots usually leaving the braincase through three foramina, two of which, the middle and the ventral (or anterior) ones, are termed hypoglossal and the dorsal (or posterior) one, cervical (Oelrich 1956, Willard 1915). The hypoglossal part has smaller fibers and innervates the tongue, only briefly communicating with the pharyngo-laryngeal ramus of the CN IX. The cervical component is morphologically very similar to the first and second spinal nerves, the first of which the dorsal ramus communicates to innervate some small neck muscles. The hypoglossal nerve may leave the braincase as a single ramus, in which case the exoccipital is pierced by only one foramen, or its anterior and posterior branches may diverge prior to exiting the cranial cavity. The plasticity of this character may however pose problems for the definition of the states, as the branches may diverge or converge along the exit route (e.g. *Euparkeria*). The number of foramina considered for coding was that seen on the external side of the braincase wall.

Optimization: The presence of two foramina for the anterior and posterior branches of the CN XII is plesiomorphic for Archosauria. A state change for a single foramen took place later in Aetosauria in the Late Triassic and in Suchia in the Early Triassic (Figure 50), while a reversal to multiple openings happened in Crocodylomorpha in the Late Triassic. A further

reversal to one foramen happened isolatedly in *Shanosuchus djadochtaensis* (LC), *Notosuchus* (LC), *Mahajangasuchus* (LC) and Thalattosuchia (EJ) – and because of the condition in these last two taxa, a reversal might be plesiomorphic to Metasuchia (EJ). In this case, multiple foramina would represent yet another reversal for later clades of Peirosauridae during the Early Cretaceous. In Dinosauromorpha (Figure 51), a single foramen occurs in *Lewisuchus* (MT) and the ankylosaurs *Tatankacephalus* (EC), *Hungarosaurus* (LC) and *Pawpawsaurus* (EC) – the last two may represent a state change for derived clades of Nodosauridae in general, in which case the two foramina of *Silvisaurus* (EC) would be a reversal. In neornithischians one foramen can be found in *Hypsilophodon* (EC), in Hadrosauridae in the Late Cretaceous (or perhaps earlier, in *Telmatosaurus*), and in *Montanoceratops* (LC). In Sauropodomorpha, one foramen is found in Macronaria starting with *Europasaurus* (LJ), in Neoceratosauria (LJ) or Ceratosauria (LT), and in *Piatnitzkysaurus* (MJ).

D i s c u s s i o n : The processes by which the ancestral two CN XII foramina were reduced to one in various saurian lineages is uncertain; possible means include having the two anteriormost roots unite, forming the anterior branch of the CN XII in archosaurs, loss of one of the anterior components, or a deviated route in the posterior branch. The morphology of the pseudosuchian braincase seems to be conservative also in the occipital area of the skull, reinforcing the idea that selective pressure on the anterior part of the braincase extends posteriorly as well – also exemplified by the suture of the exoccipital and quadrate, basisphenoid and quadrate, and the basisphenoid and exoccital at the occipital surface. This constraint was, however, broken by thalattosuchians. Finding a correlation for dinosaurs proves more difficult. Nonetheless, it is worth noticing that taxa showing state changes share a similar occipital morphology among them – and between them and crocodylomorphs. In nodosaurids, hadrosaurids, macronarians, and ceratosaurians, the braincase is highly ossified and the paroccipital processes are rather well developed ventrally, forming an occipital wall that separates the posteriormost elements of the braincase, despite not closing off the middle ear cavity. It is tempting to connect these features with well developed neck muscles for bearing the weight of an ornamented or big-sized skull, or for posture and feeding – but problems do emerge as ankylosaurids, most ceratopsians and large theropods such as megalosauroids, allosauroids and tyrannosauroids do not show a state change. Also, in dinosaurs, the trend is exactly the opposite as in pseudosuchians: while in the latter group selection seems to have been for having two well-developed hypoglossal roots, in the former it was to have only a single foramen.

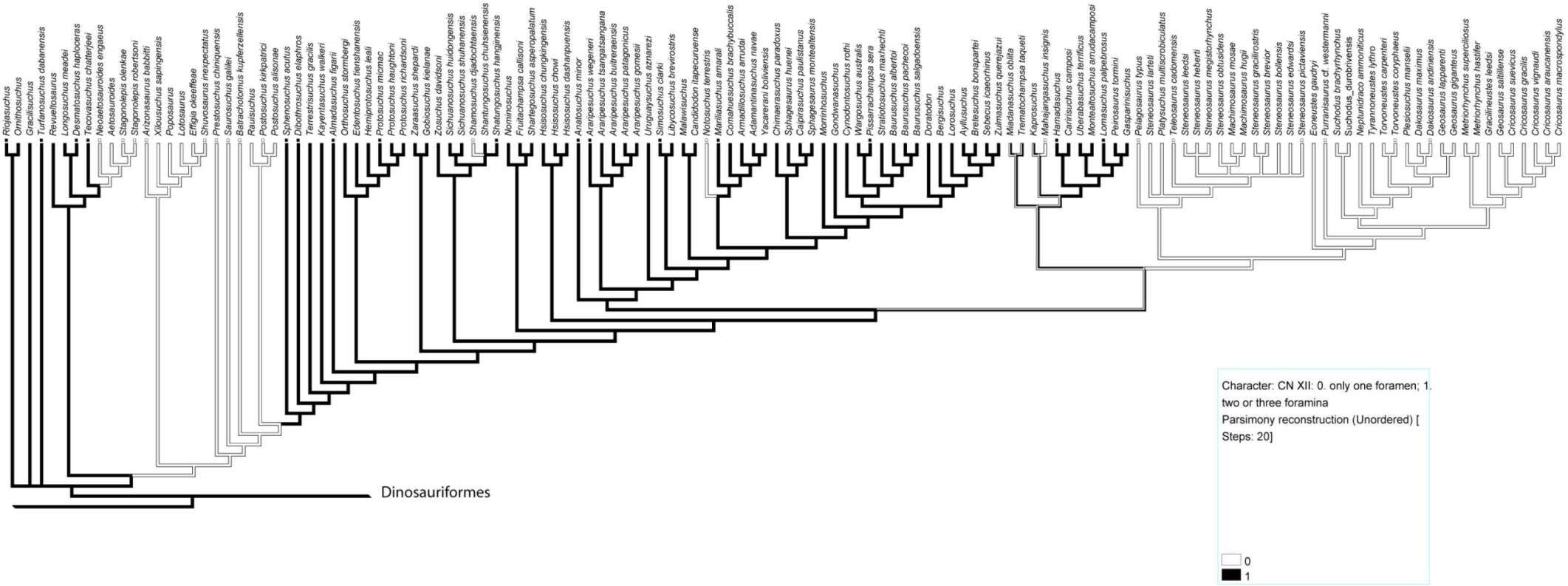

Figure 50: Optimization of character 8 for Pseudosuchia. Please refer to figure for character definition and character states.

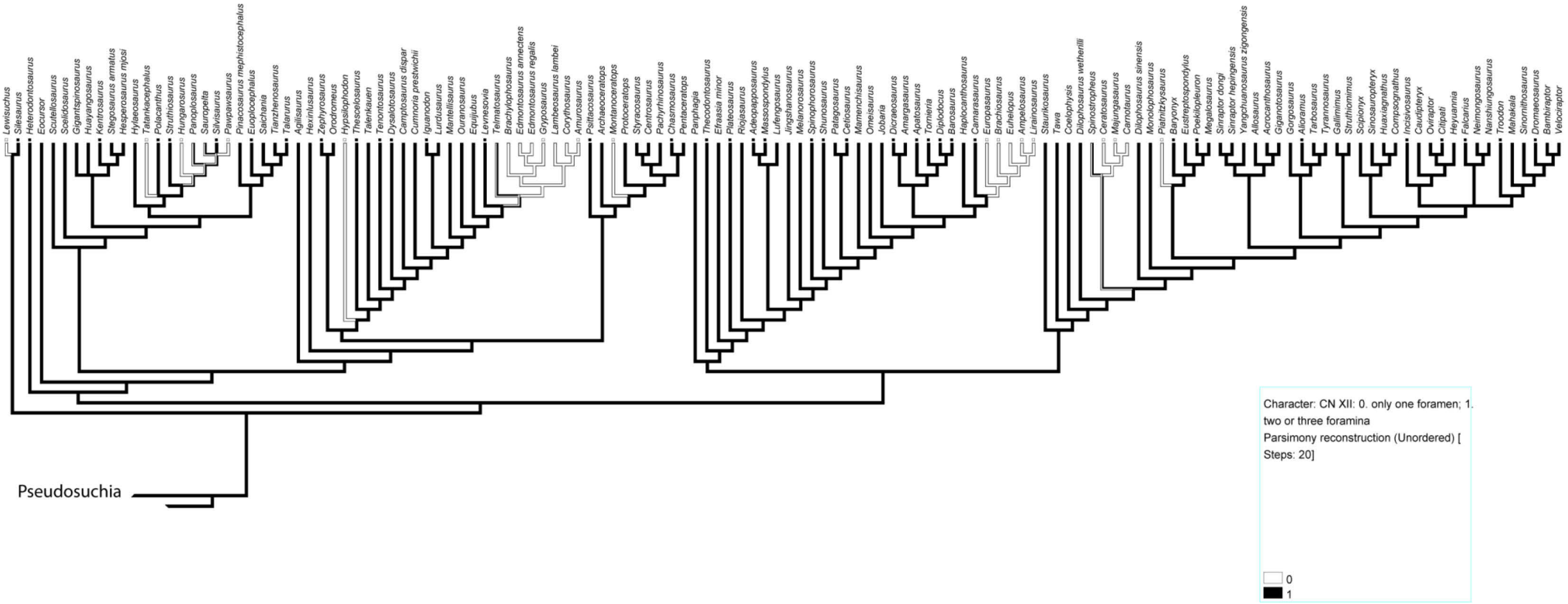

Figure 51: Optimization of character 8 for Dinosauriformes. Please refer to figure for character definition and character states.

CHARACTER 9 – ORBITOCEREBRAL VEIN FORAMEN: ABSENT (0), OR PRESENT (1).

The fenestra epioptica is located anterior and dorsal to the foramen of the CN II. This structure has been a source of major confusion since the description of sauropod braincases from Tanzania. As noted by Gower (1997), the term “fenestra epioptica” was introduced by Gaupp (1900) with no explanation as to what, if anything, it transmitted – just that it had no connection to any cranial nerve. Janensch (1935) identified a dorsal foramen on the anterior region of the braincase of *Brachiosaurus* as the fenestra epiotica, which would transmit the vena cerebralis anterior plus the CN IV. However, in *Dicraeosaurus*, it would only serve as the exit for the venous element. Janensch (1935) was subsequently followed by many other palaeontologists, especially those studying sauropods. However, the associations made among all these structures are not clearly justified. First, the fenestra epioptica is delimited by the tenia marginalis, the tenia medialis, the posterior border of the planum supraseptale, and the pila accessoria – all cartilaginous structures that remain mostly unossified in the adult. In *Sphenodon*, *Ctenosaura* and *Varanus*, for instance, the epioptic fenestra is enclosed by an imperforate membrane. Second, the existence of a vena cerebralis anterior is unlikely. In early reptile embryos, the vena cerebralis anterior extends longitudinally from the sinus longitudinalis to the anterior part of the vena capitis lateralis, and later in the embryology, it breaks in the middle into a dorsal and a ventral branch (Bruner 1907). The ventral branch retains its connection to the vena capitis lateralis, while the dorsal branch connects to the sinus longitudinalis. In squamate embryos, it does pass through the fenestra epioptica, but in archosaur taxa, the vena cerebralis anterior is lost prior to ossification – or even formation of the cartilage – of the braincase, as in mammals (van Gelederen 1924, 1925). It could be that in cases where the braincase further ossifies anteriorly, the fenestra epioptica may have left a membrane-filled opening which did not transmit any element, like the orbitocranial fonticuli of extant avialans (Baumel 1993, Gheţie 1976 – Figure 52). However, Witmer *et al*. (2008) regard this foramen as transmitting one large anastomosis between the intracranial dural sinuses and the roof of the orbit, and name the foramen as orbitocerebral foramen for a hypothetical orbitocerebral vein. Whether such an element really existed is unclear, but some taxa do present a dorsal foramen on the anterior braincase wall in addition to the trochlear nerve foramen. The nomenclature of Witmer *et al*. (2008) has been keep here, regardless of the actual function of the foramen.

Optimization: Despite the presence of this foramen in *Erythrosuchus*, the plesiomorphic condition for Archosauria is the absence of the orbitocerebral vein foramen. In Pseudosuchia (Figure 53), its presence is found in *Stagonolepis* in the Late Triassic, and could represent the state for other derived aetosaurian taxa. Because *Sphenosuchus* (EJ) also bears a

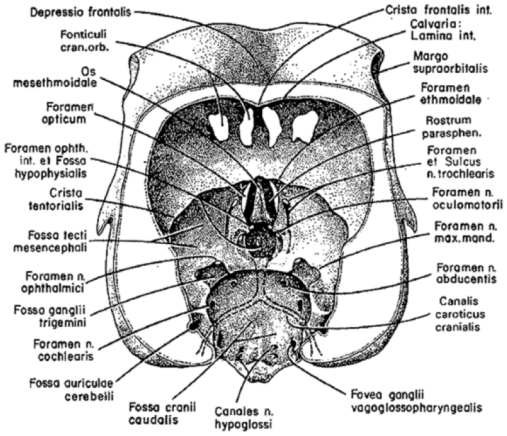

Figure 52: Medial side of the anterior braincase wall of *Columba*. Font. cran. orb.: orbitocranial fonticuli. From Baumel 1993. For other abbreviations, please refer to original paper.

foramen, but *Postosuchus kirkpatricki* and *Saurosuchus* do not, the foramen for the orbitocerebral vein could have appeared relatively early in loricatan phylogeny, in the Middle Triassic. Likewise, the presence of the foramen in *Mahajangasuchus* (LC) and its absence in *Teleosaurus* (MJ) hampers the resolutions for the remaining crocodylomorph clades. In Dinosauriformes (Figure 54), the foramen appears in Ankylosauria in the Middle Jurassic, with a reversal in *Talarurus*, ands maybe also in its sister-taxon *Tianzhenosaurus*, both in the Upper Creataceous. Because in *Levnesovia* (LC) and *Pachyrhinosaurus* (LJ) it is absent, but unknown in other ornithischians and present in both *Montanoceratops* and *Chasmosaurus*, in Ornithopoda (LJ) and Centrosaurinae (LC) it is unresolved. Likewise, in Massopoda the plesiomorphic state could not be retrieved because *Spinophorosaurus* (EJ), *Shunosaurus* (MJ), *Dicraeosaurus* (LJ) and *Barosaurus* (LJ) do not have the foramen, whereas *Apatosaurus* (LJ), *Diplodocus* (LJ), and derived clades in Macronaria do (LJ). In Allosauroidea (MJ) it is also unresolved, as the plesiomorphic state for Theropoda is the presence of such a foramen but in *Giganotosaurus* (LC) it is absent.

D i s c u s s i o n : As mentioned in the brief introduction, this character was scored regardless of the exact element it transmitted – as homologization is difficult. Some taxa do have an anterior, extra foramen, and in *Stagonolepis* (Sulej 2010), *Sphenosuchus* (Walker 2009), and *Levnesovia* (Sues & Averianov 2009) they were identified as the anterior cerebral (cranial) vein foramen. In *Mahajangasuchus* (Turner & Buckely 2008) and *Shunosaurus* (Chatterjee & Zheng 2002) it was named ethmoid artery. In *Tatankacephalus* it was identified as being the ophthalmic artery (Parsons & Parsons 2009). In *Talarurus*, an ophathalmic artery is said to be present (Tumanova 1987), but as the topographic relationships do not correspond, being located ventral on the antero-lateral braincase wall (Figure 55A), it was scored as absent.

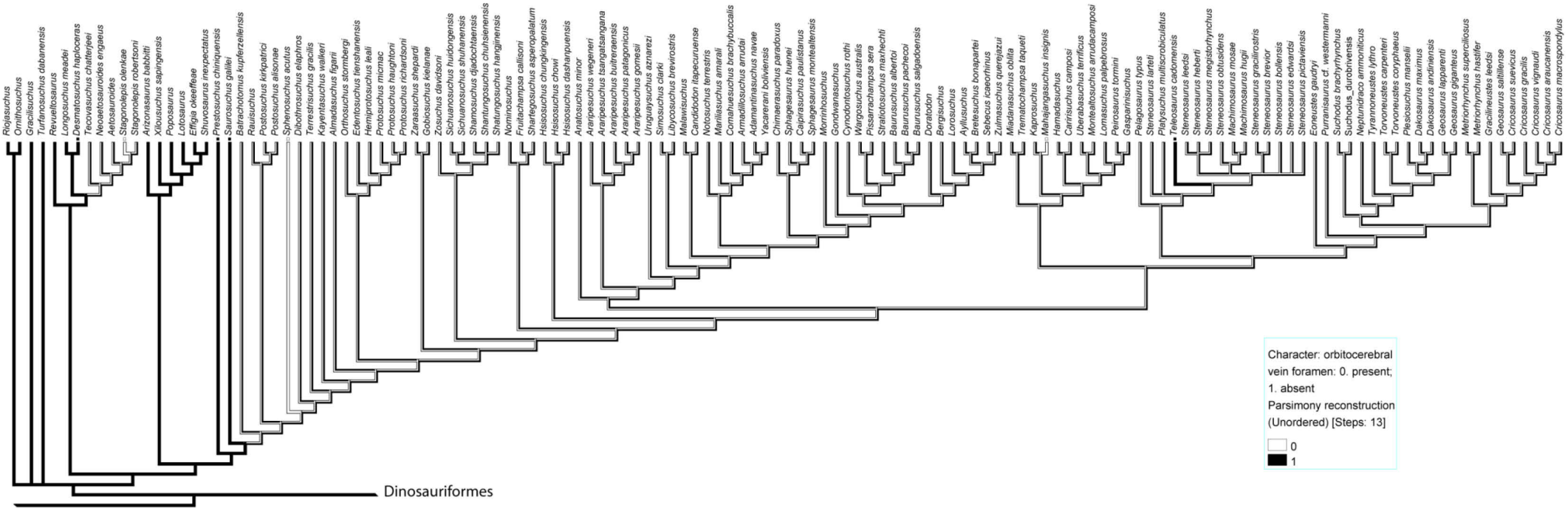

Figure 53: Optimization of character 9 for Pseudosuchia. Please refer to figure for character definition and character states.

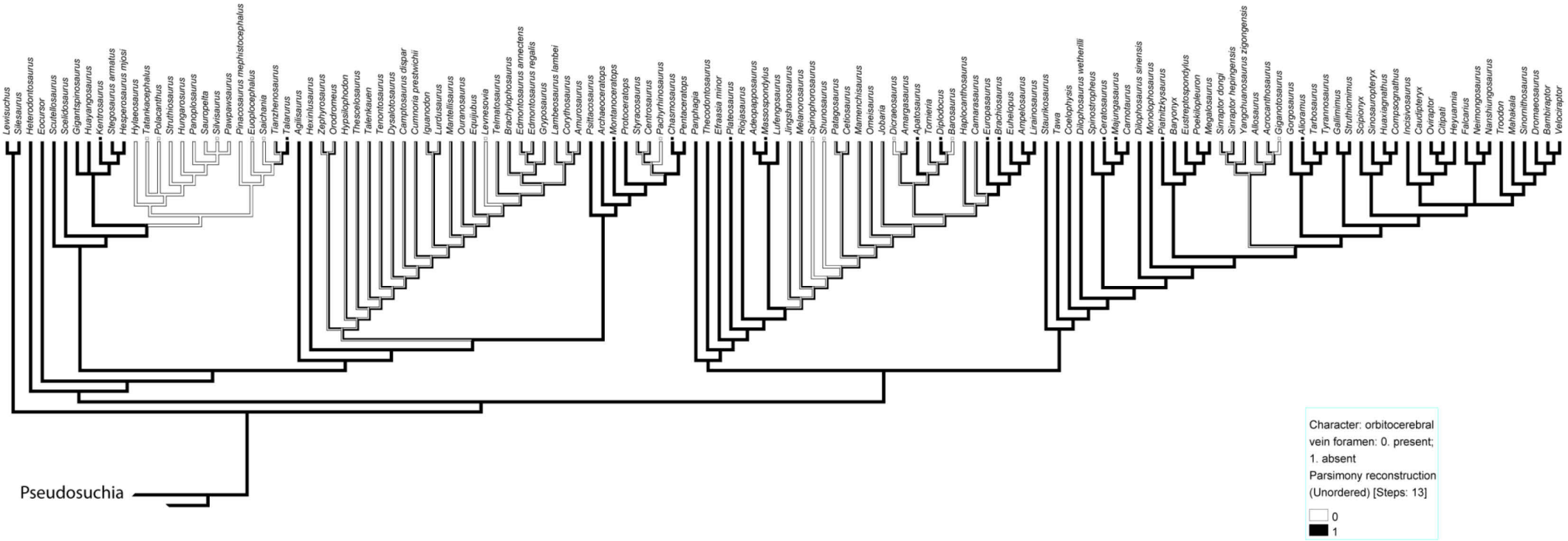

Figure 54: Optimization of character 9 for Dinosauriformes. Please refer to figure for character definition and character states.

In *Polacanthus*, three dorsal foramina were labelled by Norman & Faiers (1996) as “vcm?” (Figure 55B), and although a distinction between the middle and the dorsal cerebral veins could not be made in terms of identification, the foramen was scored as present. In *Silvisaurus*, I re-interpreted the whole series of foramina based on Miyashita *et al*. (2011). From anterior to posterior, and having figure 5 of Eaton (1960) as basis with original identification in brackets (Figure 55C), my interpretations are as follow: cerebral branch of internal carotid artery (internal carotid), common foramen for CN III and CN IV (III), foramen for orbitocerebral vein (II), foramen for abducens nerve (VI), foramen for trigeminal nerve (V), foramen for facial nerve (VII), foramen for vena cerebralis media (VI), fenestra ovalis (foramen ovalis), fenestra pseudorotunda and foramen for glossopharyngeal nerve (IX), foramen for vagus and accessory nerves (X), foramen for anterior branch of the hypoglossal nerve (XI), and foramen for posterior branch of hypoglossal nerve (XII). In *Saichania* (Figure 55D) the “vs” (venal sinus) was identified as the foramen for the orbitocerebral vein (Maryańska 1977). *Dicraeosaurus* and *Barosaurus* were scored as present based on the discussion of Witmer *et al*. (2008), and in *Giganotosaurus*, a structure present in figures 2 and 3 dorsal to the foramen of the CN IV (Coria & Currie 2002), although unidentified, were interpreted as the orbitocerebral vein foramen (Figure 55E, F).

The presence and size of this foramen has been presented as part of the evidence that sauropod braincase vasculature is particularly complex (Witmer *et al*. 2008). Although more derived macronarian clades do not possess such a vein, and if its presence alone can be used as indicative of a more developed braincase vascular system, then it is a trend that begun rather early in the evolutionary history of the clade. However, in a different context of brain enlargement and subsequent filling of the brain cavity, intricate vascular systems have also been described for hadrosaurids and for small, non-avian coelurosaurs (Evans 2005 and references therein). If, again, the presence of this foramen is at least superficially correlated with vascular development, then this trend is seen early in Ornithopoda, but not in Ceratopsia, being restricted to Centrosaurinae – but as this analysis does not include any pachycephalosaurians, and since intense braincase vasculature has been reported for them (Evans 2005), then this scenario could easily change with the consideration of additional taxa. Likewise, extant crocodilians have a complex skull vascular system very similar to avialans (Sedlmayr 2002), and many taxa do show a foramen located in the same topographic region – although rarely mentioned and with potential individual variation (Gower 1997). Thus, this trend could have begun to evolve early in crocodylomoprhs on one side of the tree, but not until coelurosaurs on the avialan side. Such a complex morphology would, however, still be lacking further support in addition to the presence of the orbitocerebral foramen in ankylosaurs (but see below), allosauroids, and crocodylomorphs – which may or may not come, if the brain did not fill the brain cavity entirely.

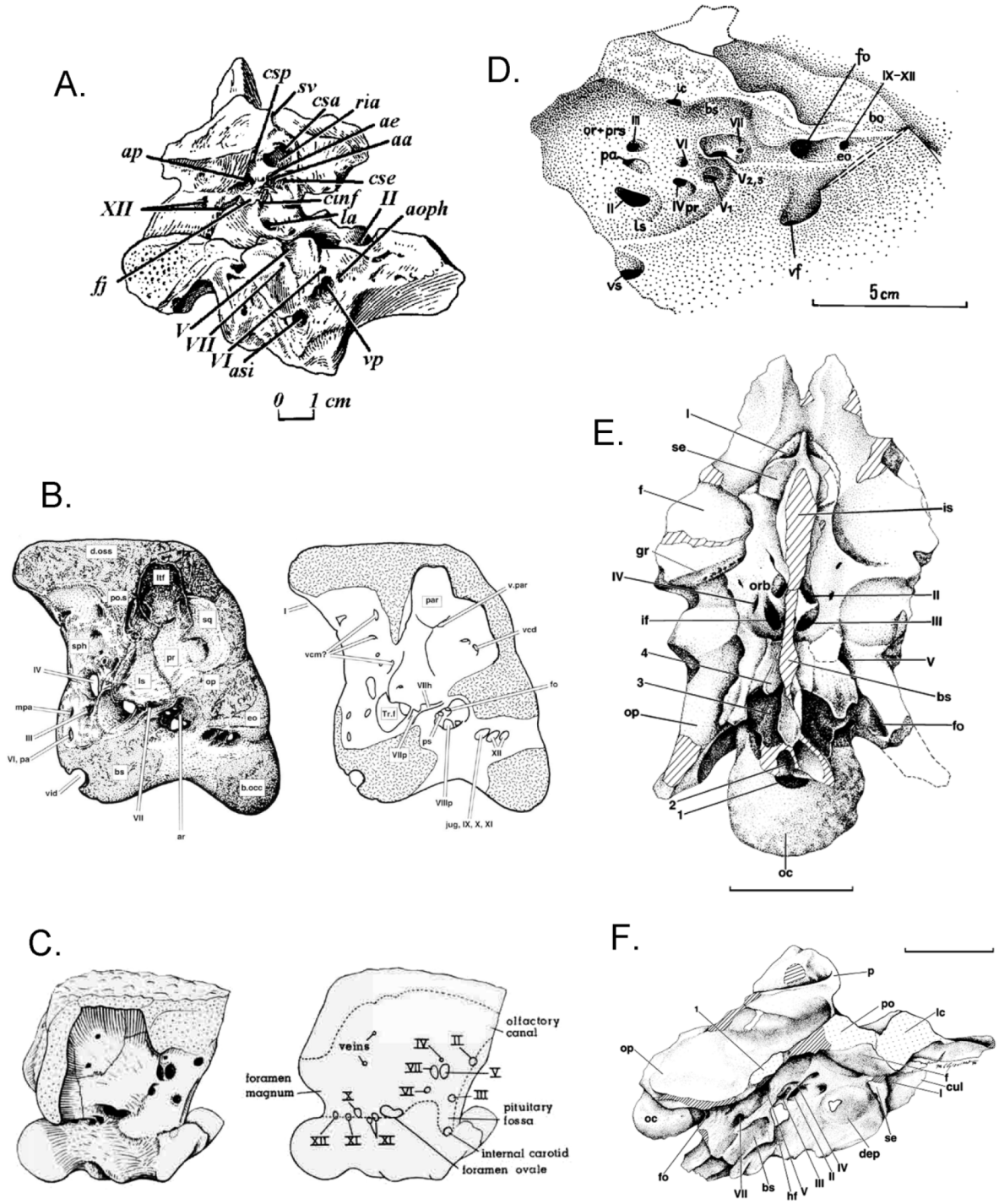

Figure 55: Dinosaur braincases. A) *Talarurus* from Tumanova 1987; B) *Polacanthus* from Norman & Faiers 1996; C) *Sllvisaurus* from Eaton 1960; D) *Saichania* (drawn upside down) from Maryańska 1977; E–F) *Giganotosaurus* from Coria & Currie 2002. See text for relevant abbreviations and discussion. For other abbreviations, please refer to the original papers.

CHARACTER 10 – INTERNAL AUDITORY MEATUS: OPEN (0), OR OSSIFIED (1).

The medial wall of the otic capsule remains unossified in many taxa, and it may serve a small compensatory role for pressure-relief in ears with a reentrant fluid circuit system. However, as explained in the introduction, the medial ossification of the otic capsule with the further development of the opisthotic and prootic provides isolation for the inner ear system from the rest of the brain, restricting and directing the path of wave travel, maximizing sound detection. It is thus considered one further step towards a more refined sense of hearing. The ossification of the medial wall of the inner ear is often termed the auditory, otic or tympanic bulla, usually in reference to the therian condition. In the latter, however, it is formed by the expansion of the temporal bone (itself the fusion of several individual bones such as squamosal, prootic and opisthotic) to enclose the ossicle chain and the middle ear cavity. Therefore, it lies external to the brain cavity.

Optimization: The internal auditory meatus is present throughout archosaurian clades, representing the plesiomorphic condition for the group (Figure 56, 57). In Pseudosuchia, an ossified medial braincase wall occurs early in Crocodylomorpha in the Late Triassic.

Discussion: As expected, this was a very difficult character to score. First because it is a difficult area to access if the braincase is articulated and the material has not been scanned – particularly difficult in pseudosuchians given their sealed anatomy. It is a character also difficult to quantify. The medial braincase wall of crocodilians is well ossified, forming a "tympanic bulla" that bulges into the cranial cavity, formed by the prootic and opisthotic. The tympanic bulla of crocodilians differs from the one of mammals in that the auditory bulla is formed by a derivate of the angular bone and represents part of the ossified middle ear cavity (Kardong 2001). Nevertheless, a internal slit-like opening still persists for the passage of the cranial nerves IX-XI, frequently termed "metotic fissure". Because many anatomical features of extant crocodilians are thought to be present early in the evolutionary history of pseudosuchians, the same terminology is often used. Not that this is not the case, but as seen in a couple of previous exemples, this can be misleading. A tympanic bulla is identified in *Stagonolepis* (Sulej 2010:871), but figure 5 indicates no extensive ossification of the medial wall – therefore it was scored as absent (Figure 58A). *Sphenosuchus* is depicted as having the medial wall of the otic region completely ossified in figures 28 and 29 of Walker (1990) – and was thus scored as present (Figure 58B). Similarly, although not very clear by the figures, in the texts a "bulla tympani" was reported for the prootic and synonymized with "cochlear prominence", and thus it was assumed the ossification of the medial wall reached far ventrally in *Shamosuchus* (Pol *et al*. 2009:29) and in *Araripesuchus tsangatsangana*

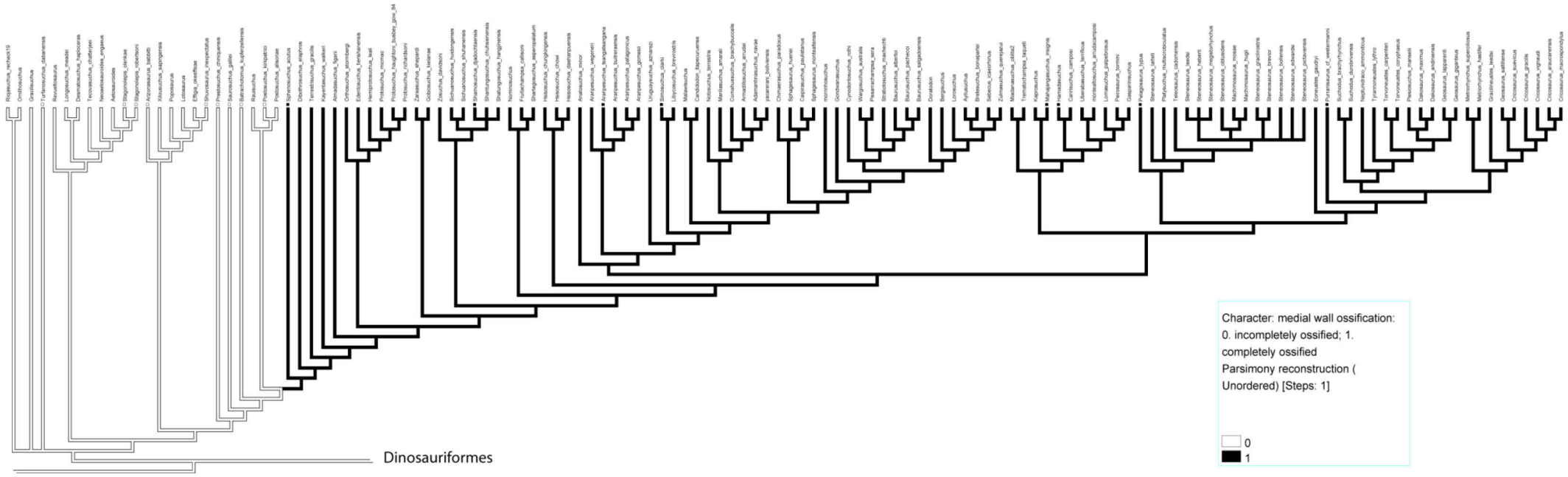

Figure 56: Optimization of character 10 for Pseudosuchia. Please refer to figure for character definition and character states.

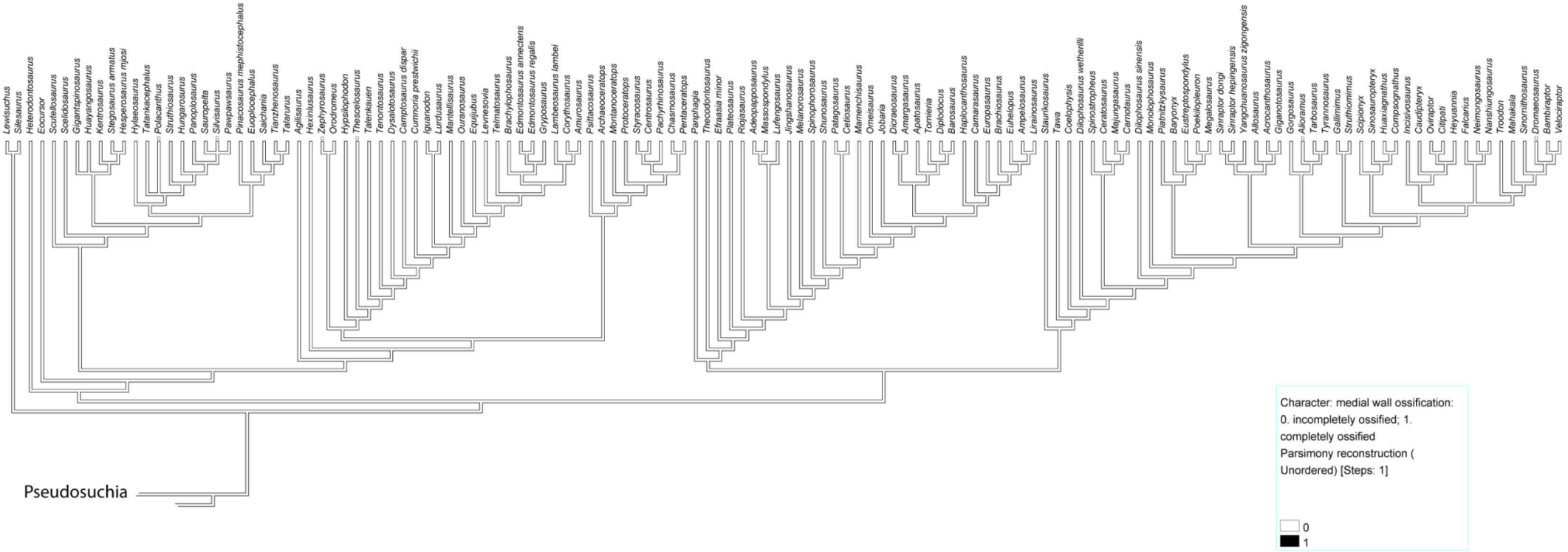

Figure 57: Optimization of character 10 for Dinosauriformes. Please refer to figure for character definition and character states.

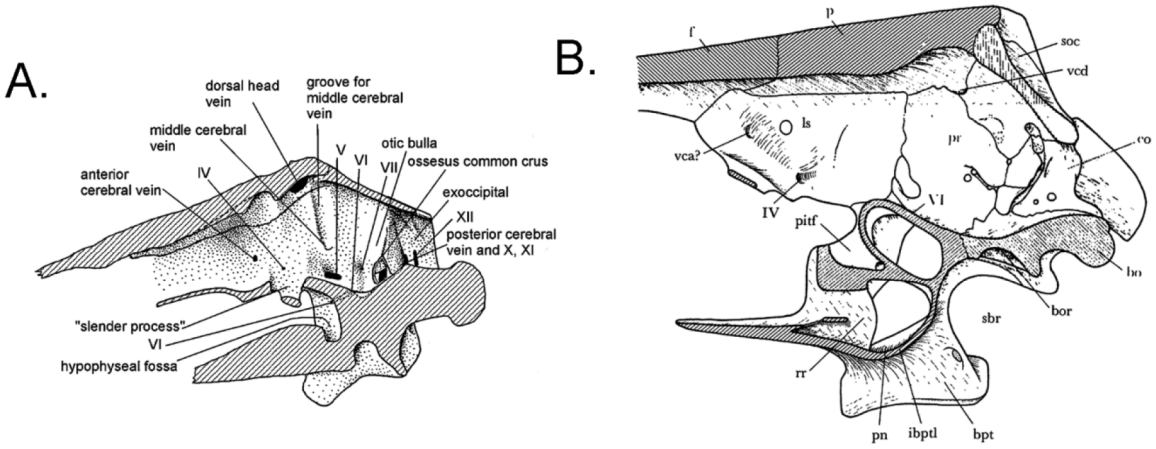

Figure 58: Medial braincase wall of pseudosuchians. A) *Stagonolopis*, unossified, from Suley 2010; B) *Sphenosuchus*, ossified, from Walker 1990. bo: basioccpital; bor: basioccipital recess; bpt: basipetrygoid process; eo: exoccipital; f: frontal; ibptl: interbasipetrygoid lamina; ls: laterosphenoid; p parietal; pitf: pituitary fossa; pn: pneumatic cavity; pr: prootic; rr: rostral recess; sbr: sub-basisphenoid recess; soc: supraoccipital; vcd: dorsal head vein. Roman numerals: cranial nerves.

(Turner 2006:284, 286). In *Simosuchus*, however, although a bulla tympani is recognised, the medial wall seems incompletely ossified in figure 19, but the text reports it is due to damage (Kley *et al*. 2010:58). It was, nonetheless, scored as ossified. The dinosaurian tympanic bulla, when present, is similar to that of crocodilians, and to that of other diapsids as for instance the iguanid *Ctenosaura* (Oelrich 1956), but intermediate morphologies have been identified. A tympanic bulla is present in the ornithopod *Dysalotosaurus* (Sobral et al. 2012:1095,1096), as more anteriorly, the prootic is developed, and thus it is possible to identify the foramina for the anterior and posterior branches of the CN VIII. However, an internal auditory meatus is still present at the medial and ventral-most portion of the vestibule and also in the area of the cochlea. As it is incomplete, the internal auditory meatus was scored as open in this taxon.

CHARACTER 11 – ANTERIOR BRAINCASE WALL: UNOSSIFIED (0), PARTIALLY OSSIFIED (1), OR COMPLETELY OSSIFIED (2).

The anterior braincase wall is composed of several cartilages that may ossify in various combined manners with adjacent cartilages to form several different elements, such as the orbitosphenoid, the laterosphenoid, and the epipterygoid. There is still much confusion regarding the homologous nature of these elements throughout vertebrate history, and it is out of the scope of this work to try to further clarify the current nomenclature. The main ossification on the anterior braincase wall in archosaurs is here termed laterosphenoid, as suggested by Clark *et al*. (1993), although in sauropod literature the most commonly used term is orbitosphenoid – though these are not the same ossification and are thus not

mutually exlusive (Bellairs & Kamal 1981). This character is, however, not related to which ossification is predominant on the anterior region of the braincase, and also not if any ossification is present at all, but to its degree of ossification as to help identify the presence and location of other anterior braincase structures. Therefore it was divided into three states: if unossified or very poorly ossified, so that anterior to the trigeminal foramen no other structure could be identified; if only partially ossified, so that notches indicate the presence and position of the oculomotor and/or trochlear nerves; and if almost or completely ossified, enclosing the trochlear and oculomotor nerves, and reaching to the optic nerves.

Optimization: The ossification of anterior braincase wall elements occurs in some taxa outside Archosauria, such as *Erythrosuchus* and phytosaurs, but not in *Prolacerta*, *Mesosuchus* or *Euparkeria*. Therefore, the ancestral state for Archosauria, as well as Pseudosuchia (Figure 59) and Dinosauriformes (Figure 60), could not be retrieved. During the Early Triassic in Suchia, however, the anterior wall becomes entirely ossified, representing the plesiomorphic state for the group and being found throughout this part of the tree. A lower degree of ossification happens during the Upper Creataceous in *Araripesuchus tsangatsangana* and in *Mahajangasuchus*, and may be present in the *Araripesuchus* genus as a whole and in Mahajangasuchidae, both in the Early Cretaceous. In Dinosauria, the plesiomorphic condition could not be reconstructed. However, an unossified anterior braincase wall appears in Silesauridae (MT) and in *Heterodontosaurus* (LT). The plesiomorphic state could also not be reconstructed for ornithischians, but extensive ossification occurs in Eurypoda (EJ), in *Tenontosaurus* (EC), in Hadrosauriformes (LJ), and later in Neoceratopsia (EC). An unossified anterior braincase wall appears in the Early Cretaceous in *Zephyrosaurus* and *Hypsilophodon* and in *Dysalotosaurus* (LJ). The plesiomorphic state retrieved for Sauropodomorpha was also an unossified anterior wall. Further ossification occurs later in Sauropoda (LT), but perhaps also earlier in Massopoda (LT). A slight reversal is seen in *Cetiosaurus* in the Middle Jurassic (and may be present in Cetiosauridae in general in the Early Jurassic), in *Camarasaurus* (LJ), and in *Ampelosaurus* in the Late Cretaceous – and perhaps later in Titanosauriformes in general in the Late Jurassic. Likewise, in Theropoda the plesiomorphic state is unknown. Anterior braincase wall ossification happens in the Late Triassic in Neotheropoda, with the branching off of Ceratosauria, and a reduction in this degree is seen in *Tyrannosaurus* (LC) – and maybe in Tyrannosaurinae as a whole.

Discussion: As mentioned in the introduction of this character, it was not intended to trace the existence of a latero- or an orbitosphenoid in archosaurs, but rather the degree of

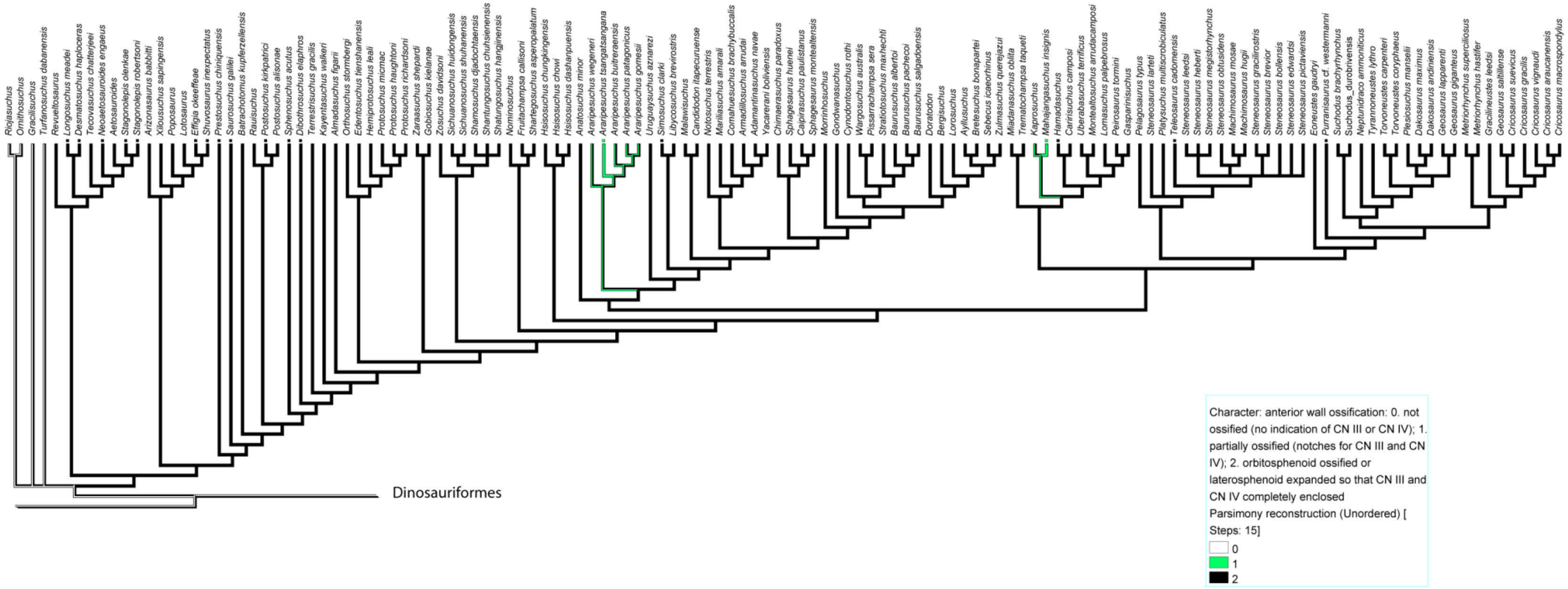

Figure 59: Optimization of character 11 for Pseudosuchia. Please refer to figure for character definition and character states.

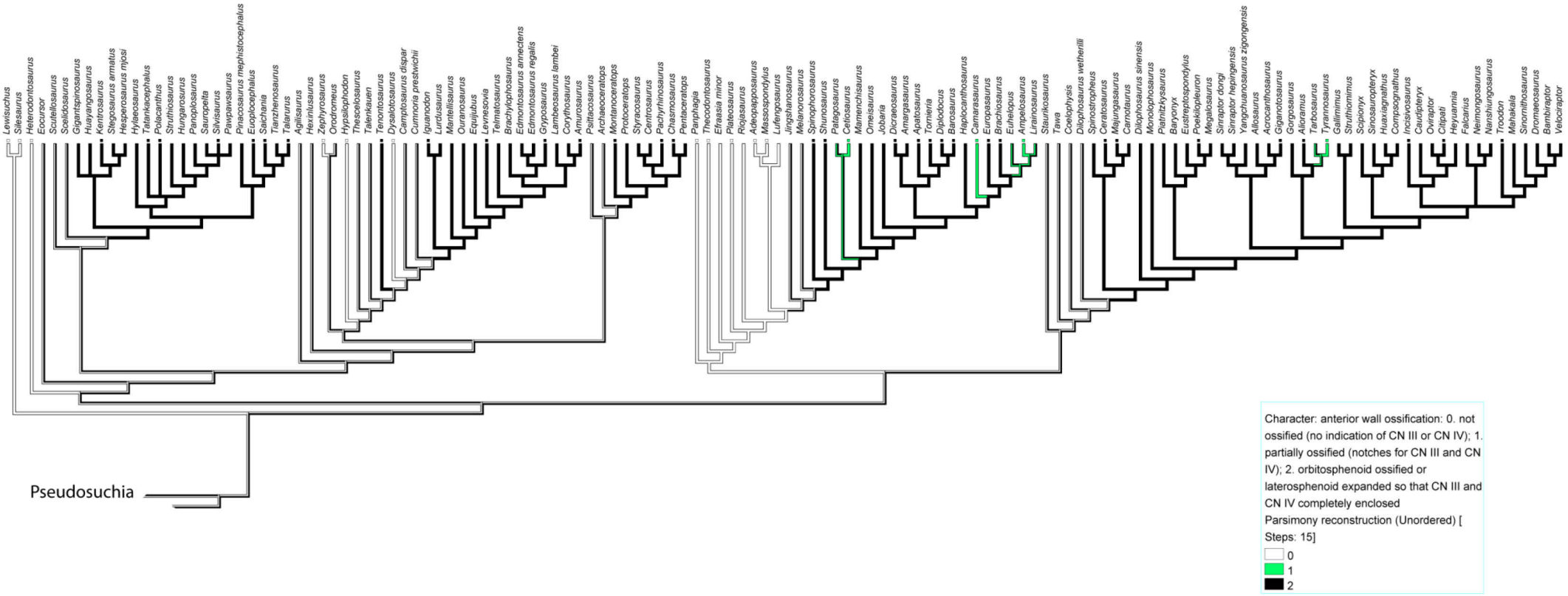

Figure 60: Optimization of character 11 for Dinosauriformes. Please refer to figure for character definition and character states.

ossification of these elements. A lateropshenoid has been documented for a number of taxa scored here as “unossified”, but it is many times restricted to the dorsal-most portion of the antero-lateral part of the braincase, so that it is of little help in the identification of structures such as the presence or location of cranial nerves. The anterior braincase wall becomes extensively ossified very early in pseudosuchian evolutionary history and remains basically unchanged in more derived clades. In dinosaurs, on the other hand, the character is a lot more plastic. Many basal taxa have a poorly ossified anterior wall, and further ossification is only found later in all major groups independently. Perhaps the exception is theropods, where a fully ossified anterior wall happens rather early in their evolutionary history. A great variety is seen in the degrees of ossification in sauropods, although a trend towards a more ossified braincase can be noticed in more derived clades.

CHARACTER 12 – SEPARATE FORAMEN FOR THE VENA CEPHALICA MEDIA: ABSENT (0), CONFLUENT WITH CN V FORAMEN (1), OR PRESENT (2).

The middle cerebral vein was discussed extensively in the previous chapter, and need not be introduced further. It usually leaves the braincase through the CN V foramen, but a separation between these two elements may occur, where the trigeminal foramen becomes partially or completely subdivided.

Optimization: The exit of the vena cephalic media from the braincase through the foramen of the CN V is plesiomorphic for Archosauria. A complete subdivision of the foramen occurs in *Desmatosuchus* and *Stagonolepis*, being plesiomorphic for most aetosaurian taxa starting in the Late Triassic – and potentially for the group as a whole in the Middle Triassic (Figure 61). A partially sub-divided foramen is found in *Prestosuchus* (MT), *Batrachotomus* (MT), *Sphenosuchus* (EJ) and *Purranisaurus* (MJ) – the latter possibly representing the ancestral state for all Thalattosuchia during the Early Jurassic. A single foramen is also the plesiomorphic state for Dinosauria (Figure 62). In Ornithischia, a complete sub-division happens in *Heterodontosaurus* (LT), in *Silvisaurus* (EC) and in later clades of Ankylosauridae (LC). The latter two occurences may indicate that completely sub-divided foramen was present in all ankylosaurians (MJ), in which case *Polacanthus* would represent a reversal in the Early Cretaceous. In Ornithopoda, two foramina occur in *Iguanodon* (LJ) and in *Telmatosaurus* (LC), and perhaps in more derived ornithopod clades in general (LJ). In this case, *Amurosaurus* (LC) would be a reversal to two confluent foramina. *Tenontosaurus* (EC) has a partially sub-divided foramen, but it is unclear if it could represent an intermediate step, where *Dysalotosaurus* would be a reversal to the plesiomorphic state. For ceratopsians, a complete separation of the elements occurs in *Pachyrhinosaurus* in the Late Cretaceous, but

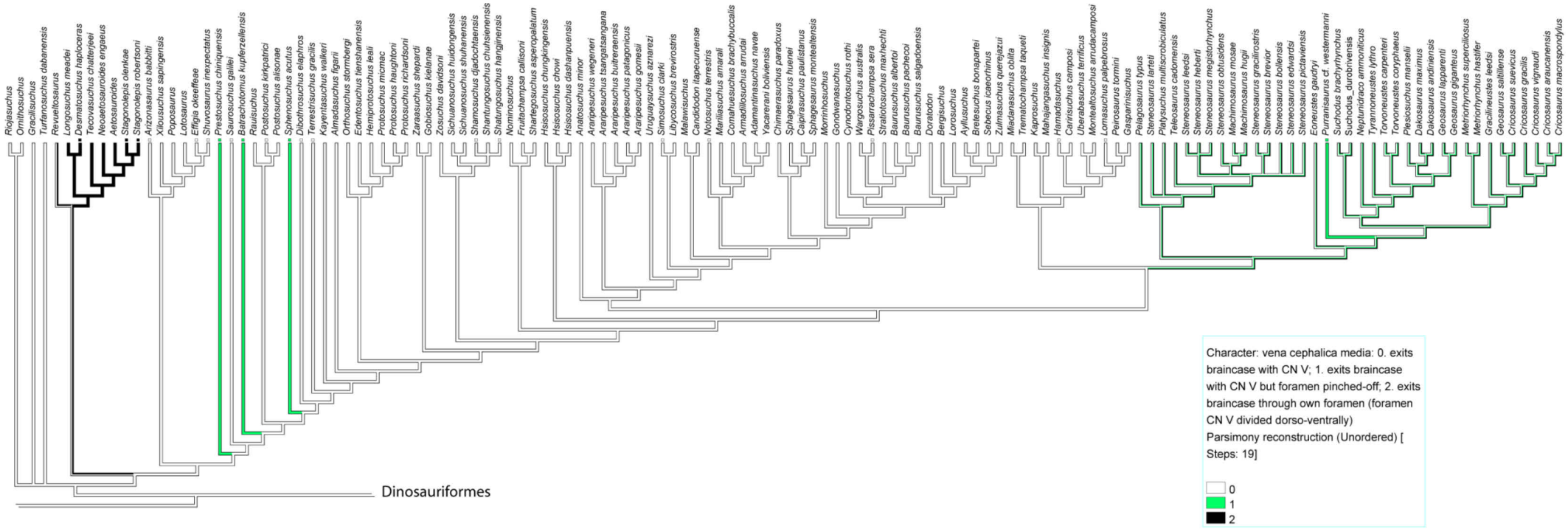

Figure 61: Optimization of character 12 for Pseudosuchia. Please refer to figure for character definition and character states.

not in *Montanoceratops*, leaving the state for other neoceratopsians unclear. A complex situation is found in Sauropodomorpha. Confluent foramina are the plesiomorphic state for the group, and occur in many basal taxa such as Massospondylidae. However, a partial sub-division in seen in *Spinophorosaurus* (EJ), obscuring the situation of derived massopodan clades in the Late Triassic. *Shunosaurus* (MJ), *Cetiosaurus* (MJ), and *Diplodocus* (LJ) have completely separated foramina, but not *Dicraeosaurus* (LJ), obscuring the state of most sauropod groups. For later macronarians in the Late Jurassic, however, a reversal to a single foramen is the plesiomorphic condition. For theropods, a partial sub-division does not occur and the complete separation of the elements happens only in particular clades, such as *Majungasaurus* in the Late Cretaceous (and maybe in in general Abelisauridae in the Late Jurassic), *Tyrannosaurus* in the Late Cretaceous (and perhaps in Tyrannosaurinae), and in *Dromaeosaurus* in the Early Cretaceous (and thus Deinonychosauria).

Discussion: The distribution of this character is very simple in pseudosuchians, and appears only in certain terminal taxa. It is possible to once again invoke the peculiar braincase anatomy of crocodylomorphs to explain a lack of morphological variation in the group, since great diversity is observed in basal pseudosuchian taxa, but in this case the constraint would have started to act prior to the emergence of Crocodyliformes. It is also interesting to notice that a different anatomy is found in Thalattosuchia. In ornithischians, the distribution of the presence of a separate foramen for the middle cerebral vein loosely coincides with the presence of the foramen for the orbitocerebral vein in eurypods and in ceratopsians. In Stegosauria, separate foramina are absent, but in Ankylosauria and Ceratopsia they are present. As mentioned in character 9, a complex and extensive vascular system has so far not been reported for ankylosaurs or ceratopsians, but if, again, the presence of exclusive foramina for the veins is correlated to any degree of vascular development, then this could be less indirect evidence of such an event in these groups. For ornithopods, however, such a correlation seems not to be present and, coincidentally or not, the diversity observed is much greater. As mentioned earlier, the partial sub-division of *Tenontosaurus* may indicate an intermediate step in the complete separation of the foramina. Similar trends are found in sauropodomorphs. First, high diversity is seen in different clades, and the indication of a partial sub-division as a necessary intermediate morphology is stronger. Second, in some sauropod taxa, a foramen for the middle cerebral vein occurs concomitantly with a foramen for the orbitocerebral vein – and are absent in more derived macronarians. However, a reverse trend is seen in Diplodocoidea: where one foramen is present, the other is absent. If the presence of a foramen is somehow indicative of element enlargement or something similar, this could suggest a transferrence of function from one vein to the other. For theropods, no such pattern could be envisioned.

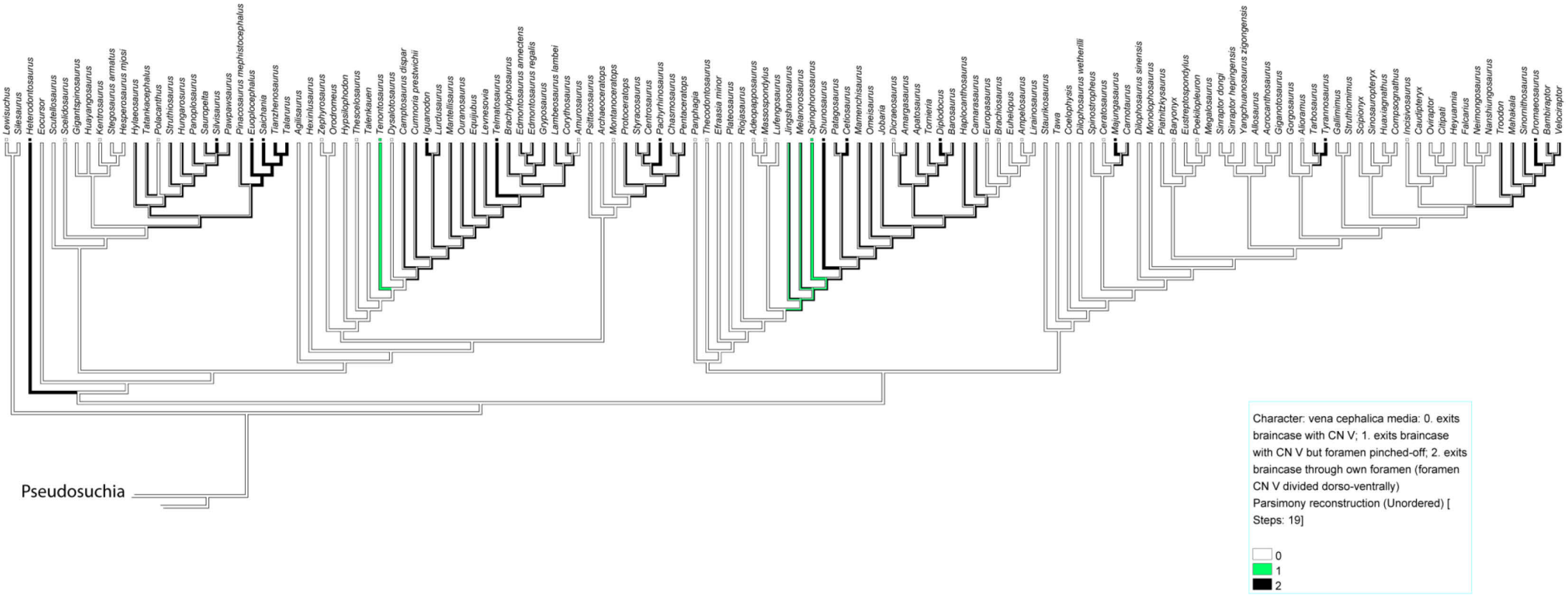

Figure 62: Optimization of character 12 for Dinosauriformes. Please refer to figure for character definition and character states.

CHARACTER 13 – CONFLUENCE OF THE VIDIAN CANALS: ABSENT (0), OR PRESENT (1).

The arteria carotis interna is the main blood supplier of the brain, originating from the dorsal aorta (Kardong 2001). In *Ctenosaura* (Oelrich 1956), at the level of the 3rd cervical vertebra, it gives rise to a lateral branch termed stapedial artery, but the main, medial branch is still called internal carotid artery. It enters the skull region at the level of the braincase floor and extends anteriorly and then slightly dorsally, passing through the vidian canal into the hypophyseal fossa, where it divides into palatine and cerebral branches or arteries. However, while this division occurs inside the basisphenoid in this case, as in squamates in general, in other amniotes this division occurs prior to the entrance of the artery in the basisphenoids (Müller *et al*. 2011). The cerebral branch joins its counterpart, forming a common basilar artery. The left and right vidian canals usually have independent courses, but they can become confluent in the basisphenoid.

Optimization: The entrance of the internal carotid artery in the hypophyseal fossa is done through two different canals in most of the taxa and this is the plesiomorphic condition in Archosauria. On the pseudosuchian side (Figure 63), a confluence between left and right vidian canals is found only in *Purranisaurus* during the Middle Jurassic. Due to the peculiar braincase anatomy of crocodyliforms, most of the taxa could not be scored, and the plesiomorphic condition for the group could not be retrieved. A single canal is also found in *Silesaurus* (UT – Figure 64), *Talarurus* in the Late Cretaceous (and perhaps for more derived clades of ankylosaurids), *Camarasaurus* (LJ), *Brachiosaurus* (LJ), and in the Middle Jurassic in *Piatnitzkysaurus* (and possibly in Megalosauroidea in the Late Triassic).

Discussion: The occurrence of this character is so punctual that, if found any physiological or developmental significance, this would pertain only to the taxa in question. The only other conclusion is the difficulty of assessing the actual morphology in crocodyliform taxa.

CHARACTER 14 – FLOCCULAR FOSSA: SHALLOW (0), OR DEEP (1).

The brain is divided in three main regions: the rhombencephalon (hindbrain), the mesencephalon (midbrain), and the prosencephalon (forebrain). The hindbrain includes the medulla oblongata, from which the roots of the cranial nerves arise, and the cerebellum. The latter has a single, medial part termed corpus, and a lateral, paired part named auricle – a part of which is termed the flocculus (Kardong 2001). The cerebellum in general has an important role in balance, emitting coordination-related responses and taking part in movement of the head and eyes. The flocculus is particularly important, as it enervated by

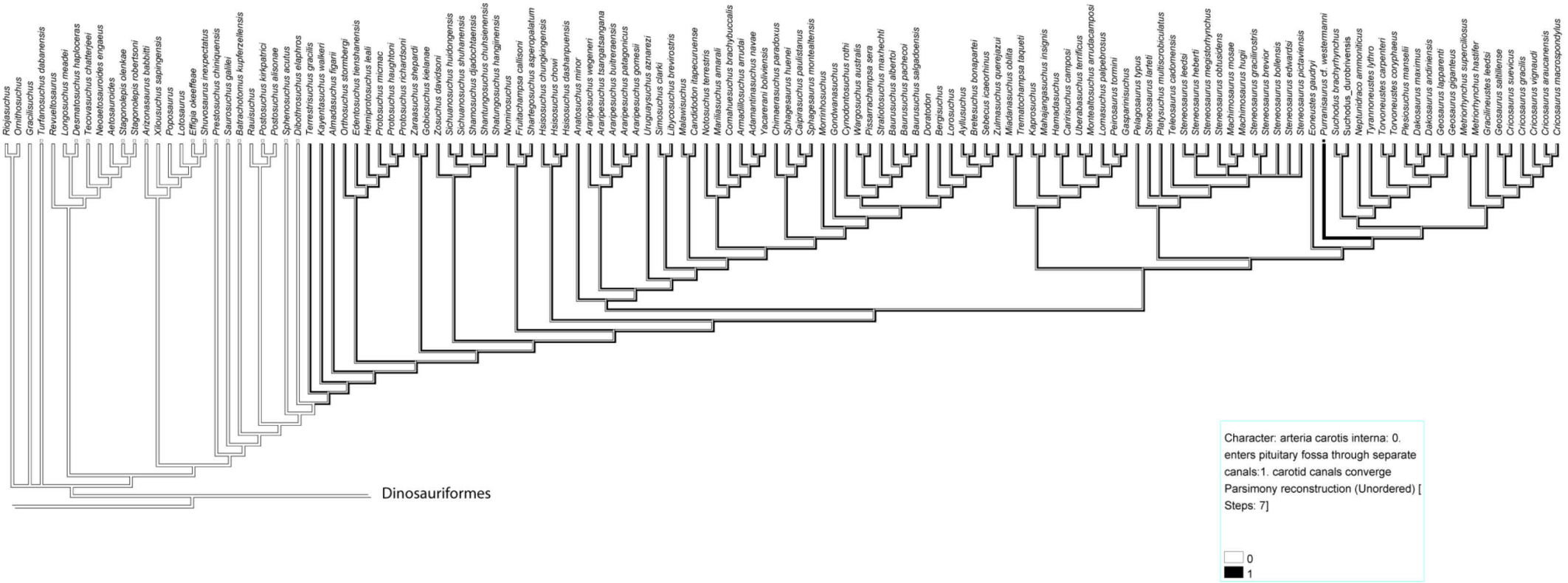

Figure 63: Optimization of character 13 for Pseudosuchia. Please refer to figure for character definition and character states.

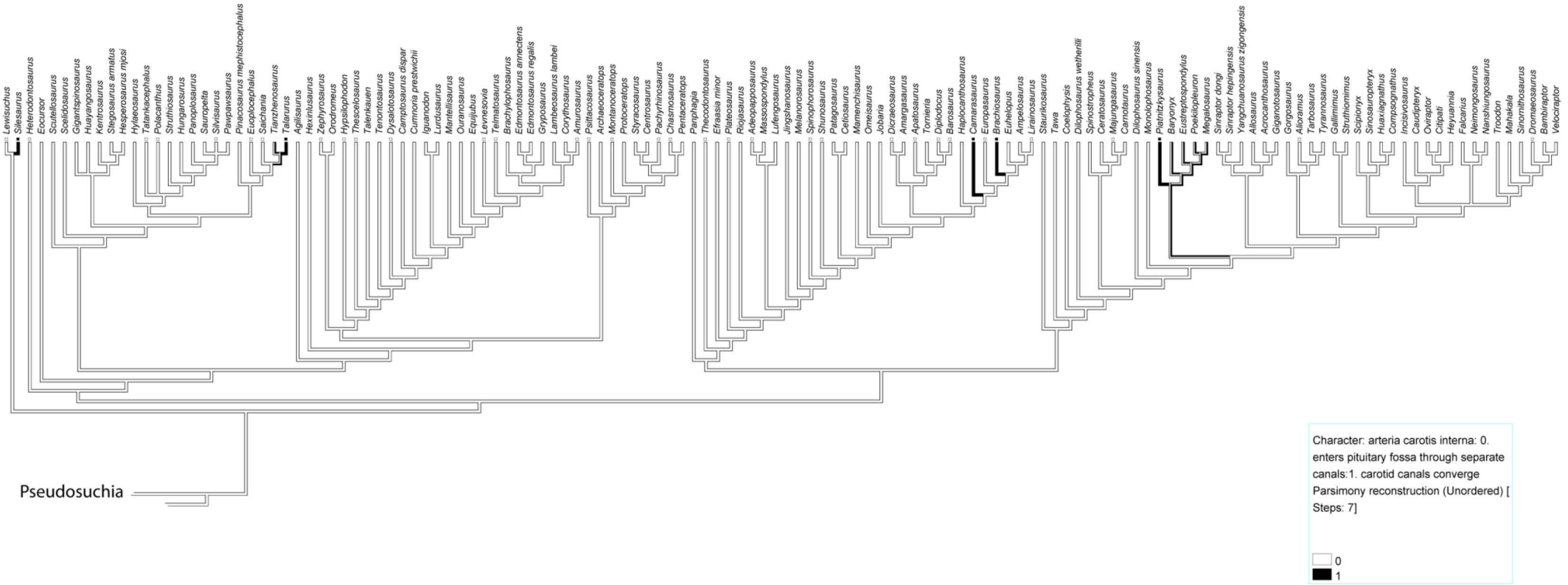

Figure 64: Optimization of character 13 for Dinosauriformes. Please refer to figure for character definition and character states.

branches from the auditory nerve (CN VIII), receiving information from the vestibule. The floccular fossa (fossa auriculae cerebelli, fovea hemispheri cerebelli, fossa subarcuata) lies on the antero-lateral region of the inner wall of the brain cavity and houses the flocculus (flocculus cerebelli, cerebellar auricle, flocculonodular lobe, vestibulocerebellum).

Optimization: The presence of a well-marked floccular fossa is plesiomorphic for archosaurs. Reductions in the size of the fossa occur in *Stagonolepis* (Figure 65) in the Late Triassic (and maybe in Aetosauria in general earlier, in the Middle Triassic), *Batrachotomus* (MT), and *Postosuchus alisonae* (LT). The plesiomorphic condition for Neornithischia is unknown (Figure 66), mostly because in *Zephyrosaurus* (EC) and *Pachyrhinosaurus* (LC) the region is not well-developed. This also hampers the situation in basal Ornithopoda and in Ceratopsia. In Sauropodomorpha, a shallow fossa is also present in *Shunosaurus* (MJ) and in Diplodocoidea (LJ), but because it is deep in *Cetiosaurus* (MJ), the situation for almost all massopodans in unknown. The same occurs only in certain terminal theropod taxa: in the Late Cretaceous, *Majungasaurus* and Tyrannosaurus have small fossae – and maybe abelisaurids and tyrannosauroids in the Late Jurassic.

Discussion: The subjectivity of this character is evident, and I found no better way to quantify it if not using “small” or “shallow” and “enlarged” or “deep” – which are usually very difficult to quantify. The floccular fossa, when significant, is a feature usually mentioned in descriptions, and facilitates the identification of the flocculus in endocasts. When I was not able to analyse the material, or when CT-scan based descriptions were available, these were my two textual indications for scoring the presence of a well-developed flocculus. A small floccular fossa has been interpreted as being correlated with a decrease in reliance on quick head movements and with less sophisticated gaze-stabilization mechanisms (Sampson & Witmer 2007). A reduced flocculus does not seem to be related to size nor to stiffness of the neck in relation to the rest of the body, which could reduce the necessity of greatly developed vestibule-occular reflexes – although this could be a particular case in sauropodomorphs and ceratopsians.

CHARACTER 15 – BRAINCASE PNEUMATIC SINUSES: ABSENT (0), MODERATELY PRESENT (1), OR BRAINCASE HIGHLY PNEUMATIZED (1).

The braincase of extant archosaurs is highly pneumatized. While these may not represent completely homologous systems, similarities occur in pseudosuchians and dinosaurs. The pneumatic system originates from epithelial evaginations that form air-filled chambers, which may or may not invade skeletal components (Witmer 1990). The air-filled chamber may be called sinus, sac, antrum, recess, space, cavity or diverticulum –

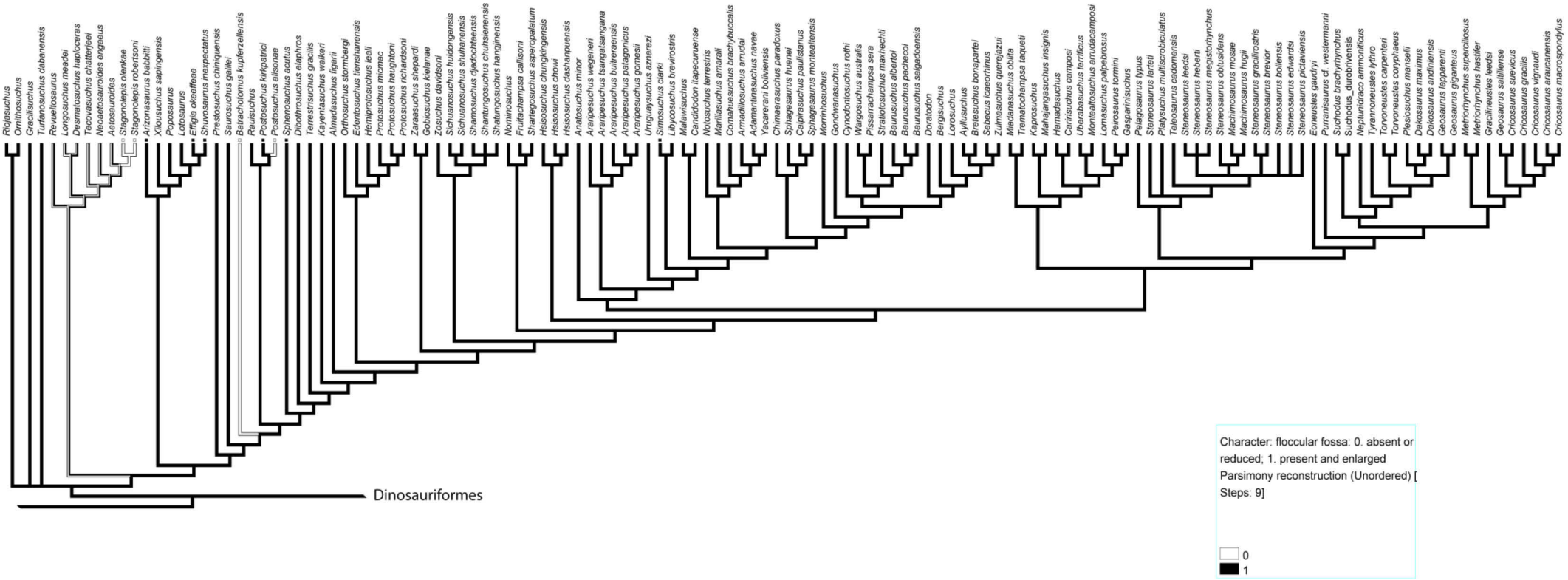

Figure 65: Optimization of character 14 for Pseudosuchia. Please refer to figure for character definition and character states.

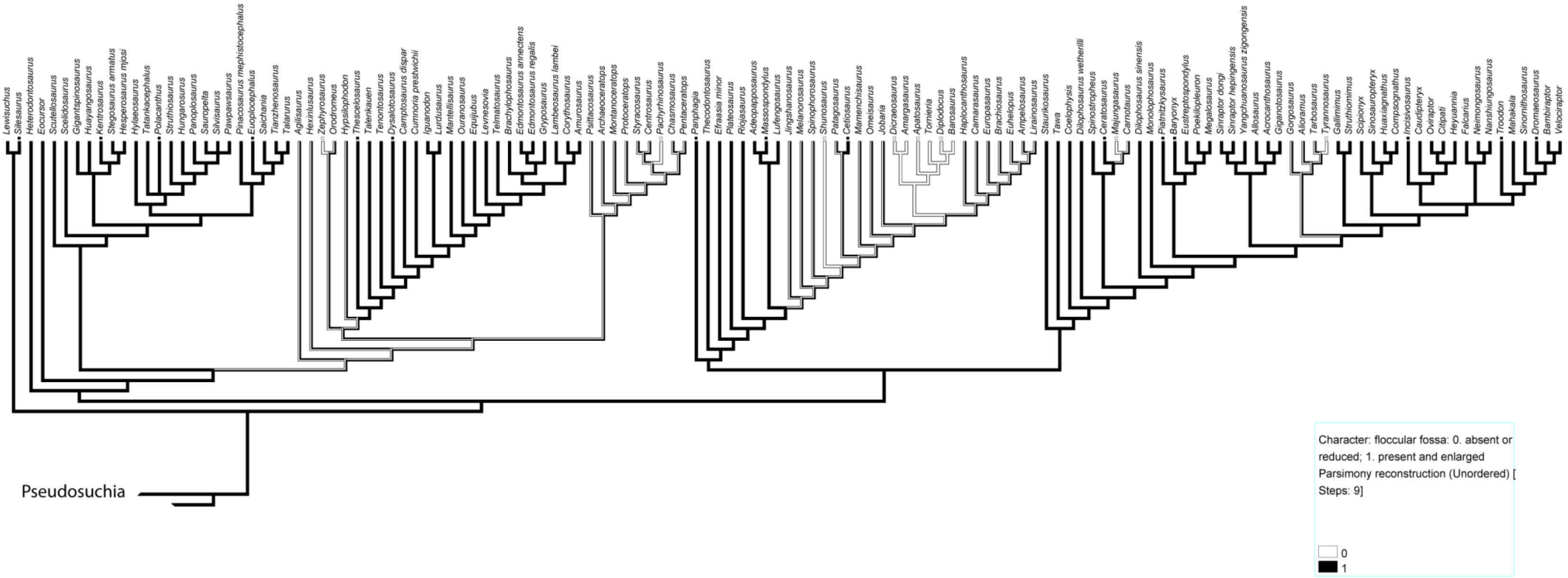

Figure 66: Optimization of character 14 for Dinosauriformes. Please refer to figure for character definition and character states.

with no difference as to location, size or system to which it may be connected. The pneumatic system present in archosaur braincases is called the paratympanic system, of which the pharyngotympanic is its main component. The middle ear cavity itself is part of this system, as it is formed by the inflation of the epthelium of the first pharyngeal pouch of the embryo. In adults, it still retains a connection with the pharynx through the Eustachian tubes. A second evagination of the epithelium of the pharyngeal pouch forms a median pharyngeal sinus that may connect to the pharyngotympanic sinus. Outgrowths of the middle ear cavity invade adjacent bones of the skull, including elements of the braincase, lower jaw, palate and orbito-temporal regions.

The brief descriptions given here will mainly follow Witmer & Ridgely (2009) on tyrannosaurs, and notes on avialans are based on Witmer (1990), and for crocodilians on Walker (1990). The paratympanic system is divided into three main parts: the pharyngotympanic (or tympanic, middle ear), the median pharyngeal and the subcondylar systems.The tympanic system has five sub-divisions: the anterior, posterior and dorsal tympanic, the quadrate and the articular recesses. Of these, only the first three will be considered, given their relevance to the area focused in this study.

The foramen of the anterior tympanic recess (ATR – sometimes also called lateral tympanic recess), is located at the level of entrance of the internal carotid artery, where the prootic, laterosphenoid and basisphenoid meet (Figure 67). This medial diverticulum is called the retrohypophyseal sinus. The posterior extension may reach the area of the basal tubera, where it communicates with the anterior and posterior basiphenoid recesses of the median pharyngeal system. Another major extension is sent dorsally (ascending diverticulum) to the laterosphenoid, and is located between the canals of the V_1 and V_{2+3}. Small extensions of the main diverticulum can be sent to between the canals of the CN VI and to the anterior region of the hypophyseal fossa, invading the cultriform process of the parasphenoid (prohypophyseal sinus). The ATR is always present in avialans, although the morphology varies according to the group. It expands antero-medially between the alisphenoid and the basisphenoid, invading both bones. Within the basisphenoid, the topology is similar to the abovementioned, albeit more posteriorly expanded. The facial nerve of avialans exits the braincase within, or just posterior to the ascending diverticulum, and its palatine ramus traverses it. In crocodilians, the ATR is absent.

The posterior tympanic recess (PTR) is the largest of the braincase sinuses. The opening foramen is located ventral to the crista prootica, at the base of the paroccipital process and postero-dorsal to the fenestra ovalis and fenestra pseudorotunda, bounded by the prootic and otoccipital. It expands dorso-laterally into the process and dorso-medially into the supraoccipital, where it is traversed by the vena capitis dorsalis and contacts its fellow.

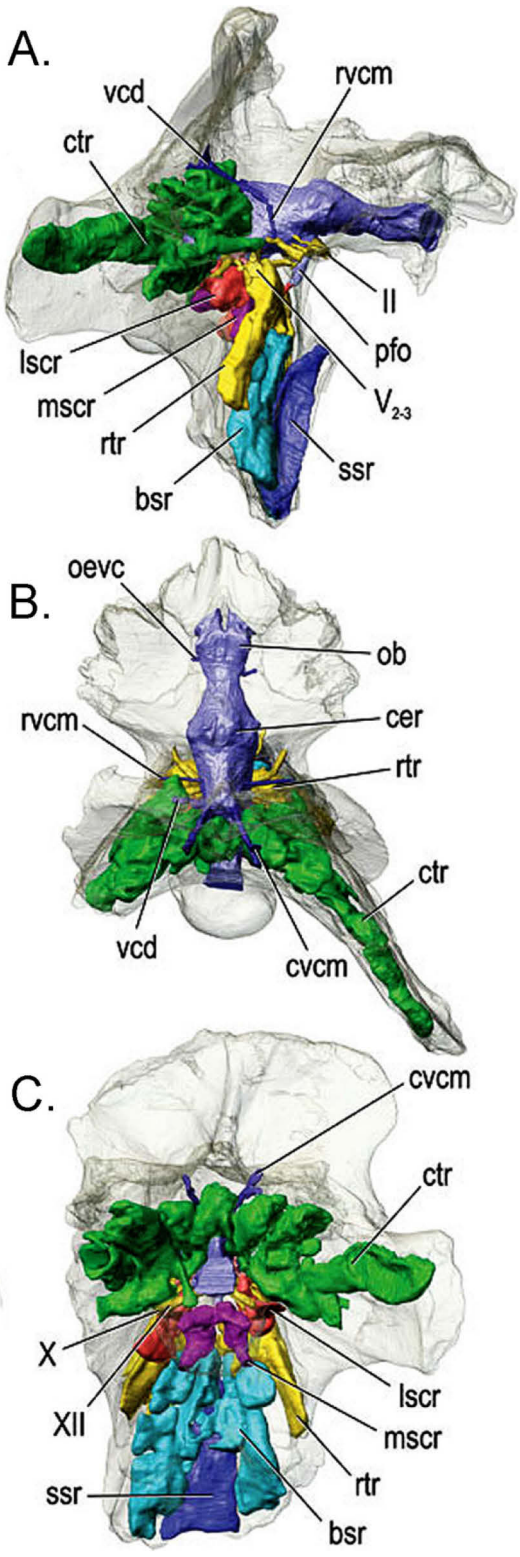

Figure 67: Braincase pneumatic sinuses of *Tyrannosaurus* in A) right lateral; B) dorsal; and C) anterior views. bsr: basisphenoid recess; cer: cerebral hemisphere; ctr: caudal tympanic recess; cvcm: caudal middle cerebral vein; lscr: lateral subcondylar recess; mscr: medial subcondylar recess; ob: olfactory bulb; oevc: orbital emissary vein canal; pfo: pituitary fossa; rtr: rostral tympanic recess; rvcm: rostral middle cerebral vein; ssr: subsellar recess; vcd: dorsal head vein. Roman numerals correspond to cranial nerves. Modified from Witmer & Ridgely 2009.

The recess may expand ventrally into the metotic strut (crista tuberalis) of the otoccipital and may communicate with the lateral subcondylar recess. Avialans have the same topology, although slightly more developed, always showing the developed ventral extension. Modern crocodilians do not have a PTR, but it is present in protosuchids and early crocodylomorphs in a very similar fashion to dinosaurs and modern avialans.

The dorsal tympanic recess (DTR) is significantly reduced in tyrannosaurids, but present in later-diverging coelurosaurs such as ornithomimosaurs and and deinonychosaurs. It originates as a dorso-medial expansion of the middle ear cavity, invading the prootic and squamosal. In many avialan groups, however, this recess forms only a fossa or depression on the dorso-lateral surface of the prootic. It may connect to the PTR in the paroccipital process and with the ATR within the prootic. In crocodilians the DTR is delimited by the squamosal, quadrate and parietal dorsally, by the prootic and supraoccipital ventrally and by the paroccipital process posteriorly. The posterior foramen of the recess (post-quadrate foramen) enters the posterior wall of the upper temporal fenestra, while the anterior one is found between the squamosal and prootic.

The median tympanic system is formed by two recesses: the subsellar and the basisphenoid. This system is absent in avialans and crocodilians, but because *Mesosuchus* seem to have developed basipterygoid diverticula with similarly positioned foramina (see Results), it is worth describing them here. The subsellar recess is more closely related to elements of the orbit and palate, but it has also connections to the anterior region of the braincase, where it forms a developed recess ventral to the hypophyseal fossa and anterior to a ventral lamina of the basisphenoid that connects left and right basipterygoid processes, and it may invade the cultriform process. The basisphenoid recess is derived from the subsellar one, and the the entrance foramen is found medially on the interbasipterygoid lamina. Within the basisphenoid, the diverticula occupy the basipterygoid processes (anterior basisphenoid sinus), although not connecting to the ATR, as well as the ventro-medial region of the bone, between the basipterygoid processes anteriorly and the basal tubera posteriorly (posterior basisphenoid sinus).

The last pneumatic group found in tyrannosaurids, the sub-condylar system, is simple and also absent in modern crocodilians and avialans, but because *Mesosuchus* exhibits intense pneumatization of the basal tubera (see next chapter), the system will be described here. In the ventral region of the basisphenoid between the basal tubera anteriorly and the occipital condyle posteriorly, there is the subcondylar fossa, where two foramina can be found.The one in the basioccpital leads to the medial subcondylar recess, while the one in the otoccipital leads to the lateral subcondylar recess. The first pneumatizes the basioccipital, including the neck of the occipital condyle, and the second enters the occipital

and extends dorsally into the metotic strut. It is unclear if the system is derived from the tympanic, pharyngeal or even from the pulmonary diverticula.

The last pneumatic system is found only in crocodilians, thus not being present in avialans, and is called the antrum mastoideum (AM). The AM is simple, and located mostly in the prootic, antero-dorsal to the fenestra ovalis, with a connection with its counterpart in the supraoccipital. The Eustachian tubes are also considered part of the pneumatic system, but they shall be described in detail in the following character.

As noted, the presence of pneumatic recesses or diverticula is not a necessary indicative of pneumatic bones, and this character relates more to the former, trying to discriminate between the different degrees of braincase pneumatization, namely a braincase without internal pneumatic sinuses, only shallow recesses on some bones, a moderately pneumatized braincase, with any one of the pneumatic systems described in the introduction, or a highly pneumatized braincase with two or more of the referred systems.

Optimization: The lack of pneumatic sinuses is the plesiomorphic condition in Archosauria. Early crocodylomorphs (Figure 68) show a high degree of braincase pneumatization in the Late Triassic, but later crocodyliform clades seem to show a reduction in this trend in the Early Jurassic. The exception is *Simosuchus* in the Late Cretaceous, which shows a reversal to a more pneumatized braincase, and which could indicate the condition for part of the notosuchian group (EC). In dinosaurs (Figure 69), some degree of pneumatization is seen in *Lirainosaurus* in the Late Cretaceous, which could indicate the state of other titanosauriforms (LJ). Although the plesiomorphic condition for Theropoda is unknown, early neotheropods show a light degree of pneumatization in the Late Triassic, and a further development in the pneumatic system is found in Coelurosauria in the Middle Jurassic. Reversals occur locally in *Poekilopleuron* in the Middle Jurassic (and perhaps in Megalosauridae in general in the Late Triassic), and in *Incisivosaurus* and *Dromaeosaurus* in the Early Cretaceous – the latter indicating the possibility of a reversal in Dromaeosauridae.

Discussion: Although difficult to asses and correctly quantify, expected diversity is found in crocodylomorphs and in theropods, since extant archosaurs have an extensively pneumatized braincase. In crocodylomorphs, there is a not so straightfowrd trend: early taxa have an extensively pneumatized braincase, which is reduced in later crocodyliforms and other mesoeucrocodylians, but re-gained in notosuchians. Thus, if the condition found in thalattosuchians represents the general trend of the lineage, then the morphology of extant clades is a reversal to a more pneumatized braincase. The potential reversal to a highly

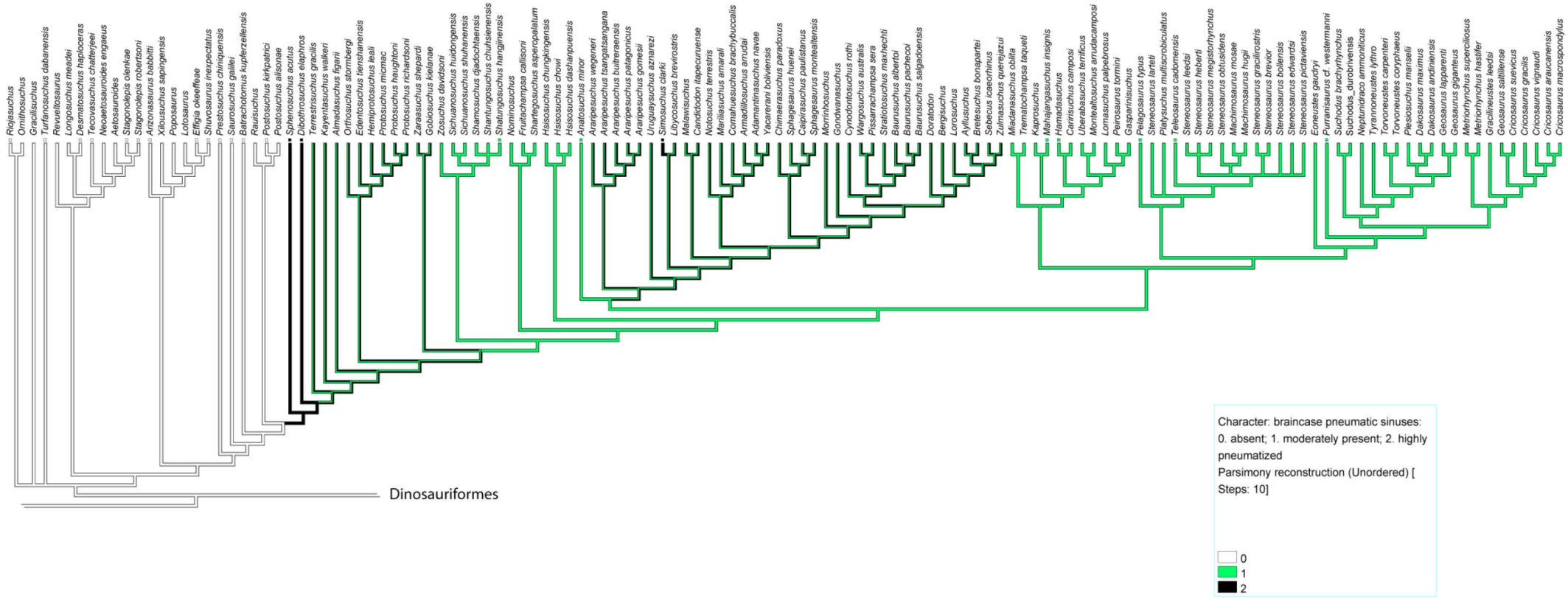

Figure 68: Optimization of character 15 for Pseudosuchia. Please refer to figure for character definition and character states.

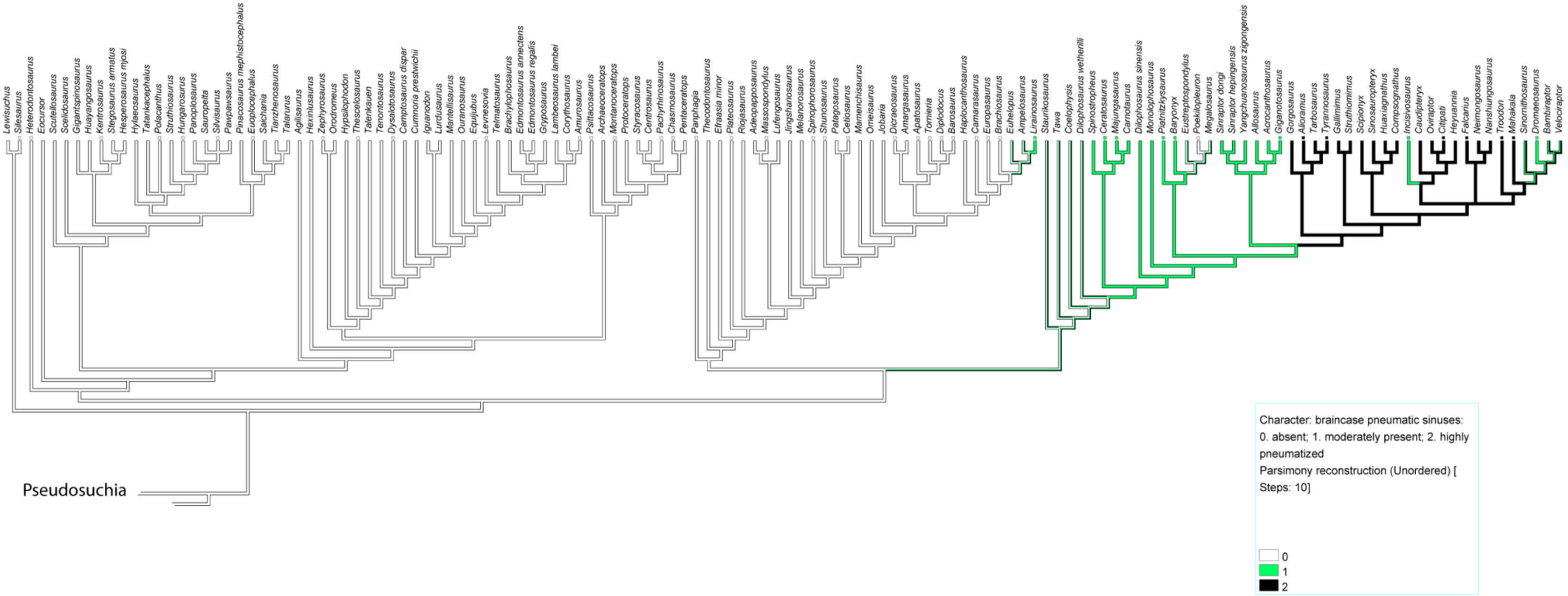

Figure 69: Optimization of character 15 for Dinosauriformes. Please refer to figure for character definition and character states.

pneumatized braincase in Notosuchia might be related to the general gracile anatomy of the group. In theropods, on the other hand, the gradual pneumatization of the braincase is evident, with reversals occuring locally in some groups. In the case of avialans, this is a trend that begins early in the evolutionary history of theropods, but more data is necessary to determine if the reversal in Dromaeosauridae is local or if it has implications for the rest of the lineage – in which case the highly pneumatized braincase of avialans would then also represent a reversal.

CHARACTER 16 – BONY ENCLOSURE OF THE EUSTACHIAN TUBES: ABSENT (0), OR PRESENT (1).

As explained in the introduction, the middle ear cavity is formed by the expansion of the first pharyngeal pouch, and a connection with the pharynx is retained by means of the Eustachian tubes. It equalizes the pressure in the left and right hearing systems and may function as a light source direction detector. All tetrapods possess a Eustachuian tube system, which is usually not enclosed by bone. An enclosed Eustachian system is found in both avialans and crocodilians, but the level of complexity of the former is not as high as of the latter. In avialans, the Eustachian (or pharyngotympanic) tubes open at the antero-medio-ventral region of the tympanic cavity, covered by the lateral and ventral wings of the parabasisphenoid, forming the basitemporal plate (Starck 1995). In crocodilians, on the other hand, the Eustachian tubes form three systems, a medial and two lateral ones. The entrance foramina of both systems, one large medial and two smaller lateral ones, are located on the braincase floor, in the suture between the basisphenoid and basioccipital, posterior to the opening of the secondary choanae. The median Eustachian tube enters the braincase floor and divides into anterior and posterior branches in the basisphenoid and basioccipital, respectively. The anterior branch divides in two lateral branches that leave the basisphenoid laterally onto the prootic and then into the middle ear cavity. Likewise, the posterior branch also divides into lateral branches in the basioccipital, leaving the bone laterally close to its contact with the exoccipital. The lateral Eustachian tubes enter through the smaller foramina and extend parallel to the suture between basisphenoid and basioccipital, their ventral half being located on the first and their dorsal half on the second, to emerge laterally on the middle ear cavity.

Optimization: The enclosure of the Eustachian tubes by the bones of the braincase floor happens only in Loricata (Figure 70), starting in *Saurosuchus* in the Middle Triassic, but a couple of punctual reversals appear, such as in *Postosuchus kirkpatricki* in the Late Triassic, which could represent the plesiomorphic state for Rauisuchia in general, in *Almadasuchus* (LJ), in *Notosuchus* (LC), and in *Purranisaurus* (MJ).

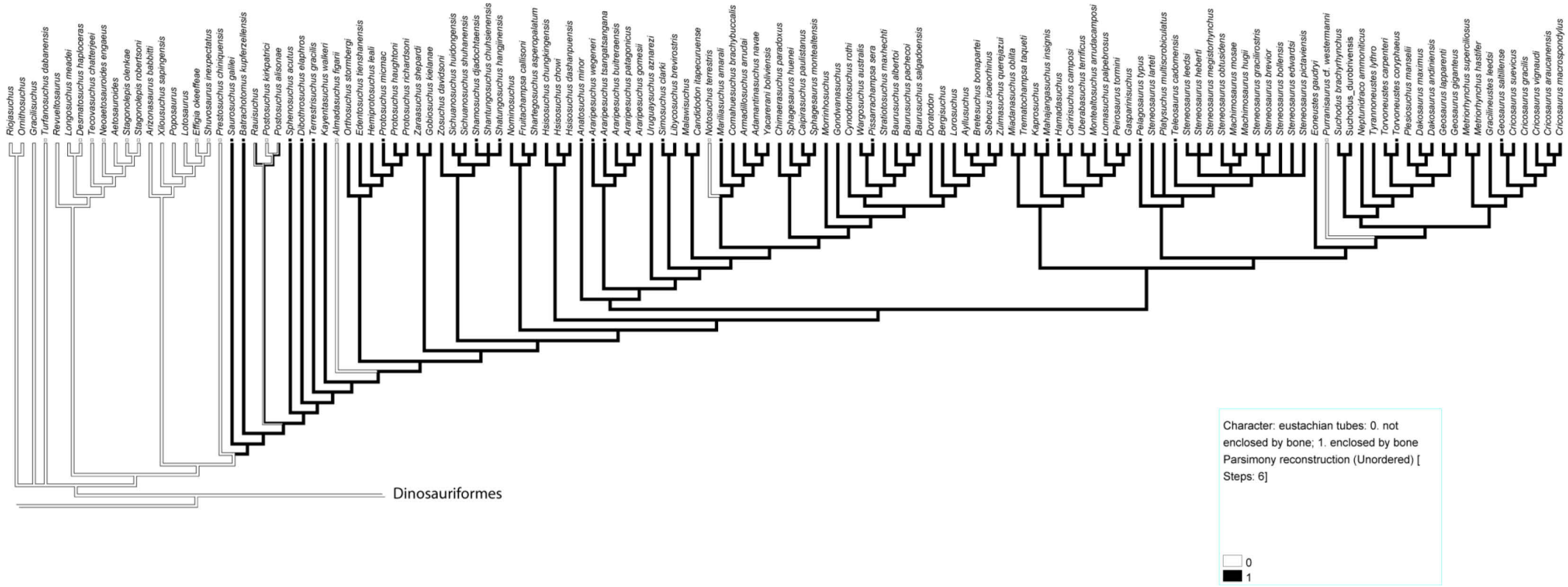

Figure 70: Optimization of character 16 for Pseudosuchia. Please refer to figure for character definition and character states.

Discussion: The bony enclosure of the Eustachian tube system starts quite early in pseudosuchians, prior to the origin of crocodylomorpha – and remain mostly unchanged in their history. It was not possible, however, to discern among the different stages in which the complexity observed in extant crocodilians was achieved. Although not belonging to the archosaurian clade, it is worth noticing here that an enclosed Eustachian tube system was not identified in *Erythrosuchus* by Gower (1997), but examination of the material BP/1/3893 suggests the presence of three foramina anterior to the basal tubera and the suture between basisphenoid and basioccipital (Figure 71). The depressions indicative of the presence of the tubes can be seen in figure 2 of Gower (1997), but they were not labelled nor identified. It is tempting to see it as belonging to a series of simple, constant development in the main lineage of pseudosuchians in which *Erythrosuchus* would not take part, but as the bony enclosure of the tubes in this taxon seem to have evolved independently, it has no consequences for the evolution of the system in pseudosuchians and represents a convergent event. In avialans, the enclosure of the proximal part of the Eustachian tube does not take place at any point in the observed evolutionary history of non-avian theropod dinosaurs, and must have occurred well into Avialae.

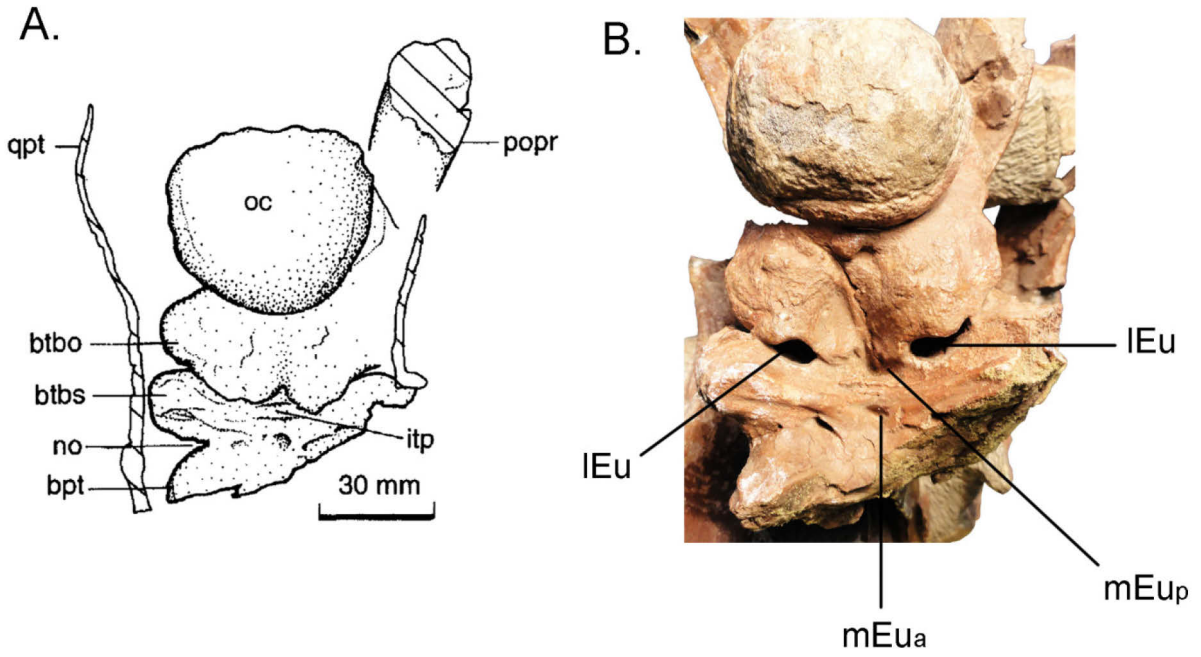

Figure 71: Braincase of the archosauriform *Erythrosuchus africanus* BP/1/3893. A) As interpreted by Gower 1997, without openings for the Eustachian tubes; B) Photography taken by me with indication of the actual openigns. bpt: basipterygoid process; btbo: basal tuber of the basioccpital; btbs: basal tuber of the basisphenoid; itp: basisphenoid intertuberal plate; lEu: openings of the lateral Eustachian tubes; mEu: openings of the median Eustachian tubes (a: anterior, p: posterior); no: notch; qpt: quadrate ramus of the pterygoid.

CHARACTER 17 – LOCATION OF THE ENTRANCE OF THE CAROTID CANALS ON THE BASISPHENOID: VENTRAL (0), OR LATERAL OR POSTERO-LATERAL (1).

As mentioned previously, the internal carotid arteries enter the hypophyseal fossa through the vidian canals, at the base of the basipterygoid processes of the basisphenoid, which may become confluent in some taxa. In some groups, the canals pierce the braincase floor ventrally, but in others it does so more laterally. Here a distinction between a completely lateral or a more postero-lateral perforation was not made.

Optimization: The lateral entrance of the internal carotid canals is the plesiomorphic condition for Archosauria and, in general, a reversal to more ventrally located foramina happens isolatedly in some taxa (Figure 72, 73), such as *Arizonasaurus* (MT), *Silesaurus* (LT), which could represent a reversal for Silesauridae (MT) in general, *Polacanthus* (EC), *Diplodocus* (LJ), and *Europasaurus* (LJ). In theropods, the ventral piercing of the arteries is found in *Incisivosaurus* and *Falcarius* in the Early Cretaceous, but because *Dromaeosaurus* (EC) shows the ancestral state, and the relationships of Oviraptorosauria, Therizinosauria and Deinonychosauria are unresolved, the condition of Maniraptoriformes (LJ) becomes unresolved.

Discussion: The ventral entrance of the internal carotid arteries in the basisphenoid have been recognised as present in all non-archosaur archosauriforms (Nesbitt 2007). However, Nesbitt (2007:302), in the context of the specific phylogenetic relationships of *Effigia*, highlights that laterally piercing vidian canals are characteristic of other “suchian archosaurs”. While not being wrong, the mapping of this character has shown that this is a condition of archosaurs in general, not being restricted to one of its lineages. The ventral location of the entrance foramen of the internal carotid artery is actually plesiomorphic for amniotes, and a change to a lateral foramen also happens independently in squamates and parareptiles (Müller *et al*. 2011). The potential reversal to a ventral position in more derived clades of theropods is intriguing, since avialans also display the plesiomorphic archosaurian condition. If a reversal really takes place in Maniraptora and is not a local trend observed in Oviraptorosauria and Therizinosauria, then a further state change must have taken place later in Avialae. It is currently unknown what types of selective forces would underlie changing direction of the course of the internal carotid arteries, but it has apparently been responsible for convergent morphologies in several diapsid groups. This is a trend that has begun prior to the origin of archosaurs, as it is present in the probable non-crown group archosauromorph phytosaurs.

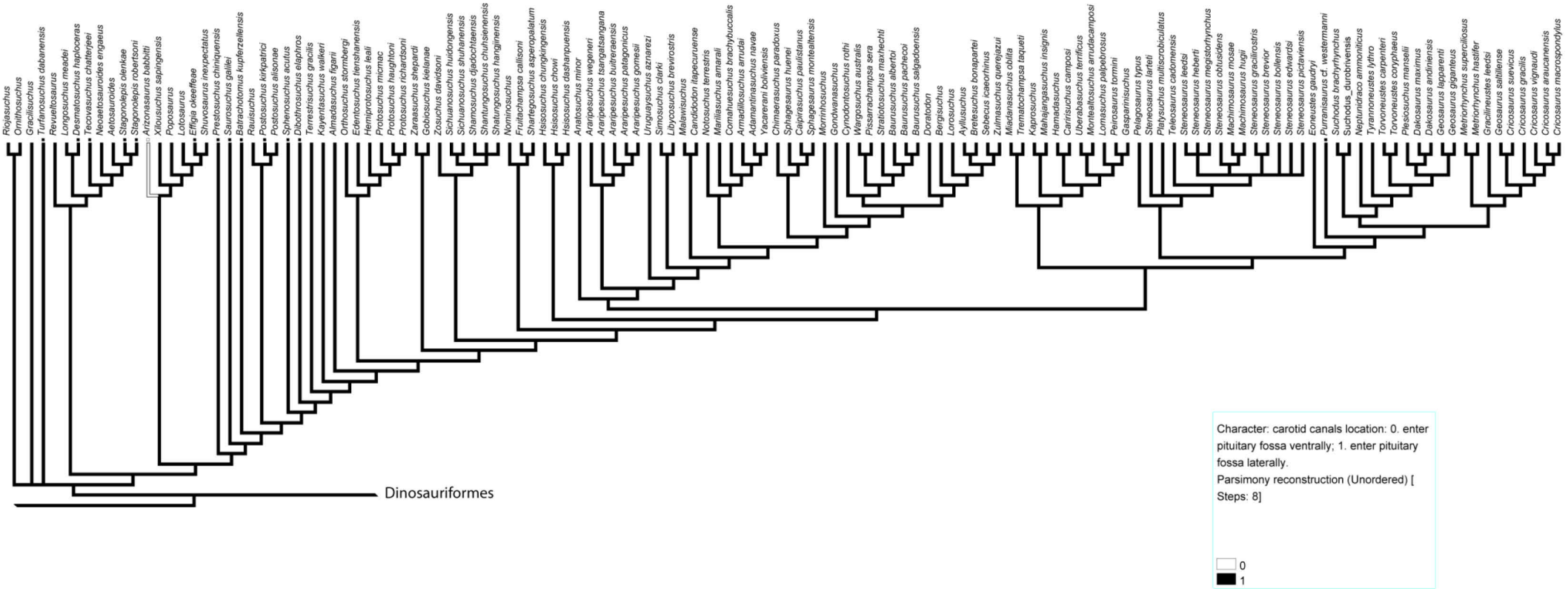

Figure 72: Optimization of character 17 for Pseudosuchia. Please refer to figure for character definition and character states.

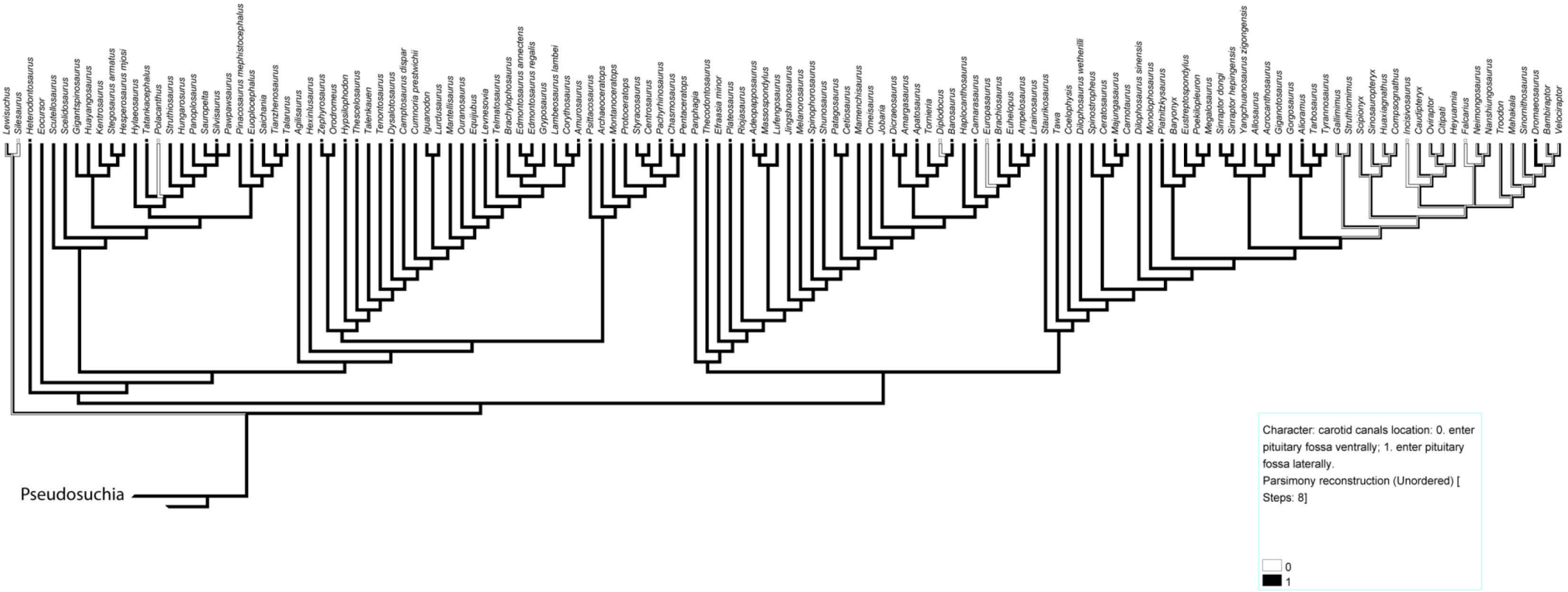

Figure 73: Optimization of character 17 for Dinosauriformes. Please refer to figure for character definition and character states.

TRAIT EVOLUTION

For this section, all state changes were counted in order to evaluate when they happened in archosaur history. For this purpose, terminal taxa were considered only when they represented an independent change not part of a more inclusive group – i.e. two state changes were computed for, for instance, *Alioramus* and *Majungasaurus* when these represented independent events, but only one change was recognised if the state was plesiomorphic for Neotheropoda. Furthermore, only actual changes were computed, not potential ones.

Most of the state changes occur in the Upper Ctreatceous (69), followed by Late Jurassic (39), Early Cretaceous (33), Late Triassic (28), Middle Jurassic (27), Middle Triassic (12), Early Jurassic (11), and Early Triassic (3). As expected, if separated by clade, Dinosauriformes accounts for most of the changes, 162, in contrast to the 52 seen in Pseudosuchia. Also as expected, Dinosauriformes is responsible for the ranking of the times for archosaurs, with most changes occurring in the Late Cretaceous (50), followed by the Late Jurassic (38), Early Cretaceous (29), Middle Jurassic (23), Late Triassic (12), and Early Jurassic and Middle Triassic (5). The exception is the Early Triassic, with no changes computed in this time in the group. On the other hand, in Pseudosuchia, most of the changes occur in the Late Triassic (16), followed by the Late Cretaceous (10), Middle Triassic (7), Early Jurassic (6), Early Cretaceous and Middle Jurassic (4), Early Triassic (3), and Late Jurassic (1).

In an attempt to separate the changes by major dinosauriform clades, nodes were classified by one of the following main groups: Anklyosauria, Ceratopsia, Ornithopoda, Sauropodomorpha and Theropoda. Changes occurring in higher or more basal ranks than these, as for instance, Eurypoda or Silesauridae, were not computed. The clade with more state changes was Sauropodomorpha (50), followed by Theropoda (39), Ornithopoda (26), Ankylosauria (20), and Ceratopsia (13) – a total of 59 changes for ornithischians and 89 for saurischians. Of these, sauropodomorph changes occur mostly in the Late Jurassic (29), theropod ones in the Late Cretaceous (16), ornithopod in the Late Cretaceous (12), ankylosaur in the Early Cretaceous (10), and ceratopsian in the Late Cretaceous (12) – and thus most changes happening in the Late Jurassic in saurischians and in the Late Cretaceous in ornithischians. A similar attempt for pseudosuchian clades was much more difficult, since clades rarely radiate into groups of similar or equivalent cladogenetic diversity – a topic that will be discussed with greater depth in the next chapter. In any case, groups were divided in Aetosauria, Rauisuchidae, Notosuchia, Peirosauridae, Prestosuchidae and Thalattosuchia. The more plastic clades in terms of braincase morphology had a total of 6 state changes: Aetosauria in the Late Triassic, Notosuchia mostly in the Late Cretaceous (5),

and Thalattosuchia mostly in the Middle Jurassic (4). They were followed by 5 state changes in Peirosauridae mostly in the Late Cretaceous (4) and Rauisuchidae in the Late Triassic, and by 4 state changes in Protosuchidae mostly during the Early Cretaceous (2).

The results of these investigations indicate that most of the changes occurring in braincase anatomy did not take place early in the evolutionary history of Archosauria, but rather late instead. As mentioned, Dinosauriformes dominates the pattern for archosaurs in general, with most of the changes occuring in the Late Cretaceous. In contrast, many braincase anatomical changes occur early in pseudosuchians, during the Late Triassic. In this analysis, it is also prior to the origin of Crocodylomorpha, indicating that the strong morphological constraint that appeared in Crocodyliformes were already acting prior to the origin of the group. The number of state changes in dinosauriforms is three times higher than the one in pseudosuchians, and also reiterates the concept that dinosauriform braincase was allowed a much greater plasticity. Surprisingly, despite the lower general morphological disparity seen in the body form of sauropodomorphs, the high number of state changes in the group indicate a strong plasticity in braincase anatomy. Ankylosaurs and ceratopsians are the groups with the lowest number of changes, and this fact may be correlated to the dorsal armor and skull ornamentation, respectively. Derived ornithopods also show diverse and complex skull ornamentation, but changes occur prior to the origin of hadrosaurs. Since the early evolutionary history of the group is better covered in this analysis, in contrast with the two previously cited groups, the character changes are also better documented.

In pseudosuchian clades, it is surprising to observe several different groups showing a very similar total number of state changes. Although the concept of low morphological disparity in the group has been challenged, most of the categories used here to assess changes were classically seen as morphologically conservative groups. The relatively high number of changes indicates that braincases were as diverse as general body forms. The exception is notosuchians, which are usually aknowledged as a morphologically very diverse group (Stubbs *et al*. 2013). Thus, it is not surprising to see a corresponding amount of plasticity in braincase anatomy. Thalattosuchians in contrast, due to their aquatic habits, are also usually seen as a very conservative group in terms of morphology. While it is true that, on the one hand, most changes occur very early in the history of the group in the Middle Jurassic and, on the other, that only a limited number of thalattosuchians were scored, it is still remarkable that the group seems to break many constraints imposed by the peculiar braincase anatomy of crocodyliforms, as did notosuchians. The high score of aetosaurs is likewise very surprising, since the group is rarely given any attention in terms of morphological diversity. It is important to recognise that most of the total number of changes in Pseudosuchia occur only in certain terminal taxa in these different groups, and cannot be considered significant for the overall evolutionary history of crocodilians. However,

considering that two of the groups with the highest number of state changes, Notosuchia and Thalattosuchia, are both crocodyliforms, it seems reasonable to recognise these as breaks in the constraints imposed by cranial akinesis.

IMPEDANCE-MATCHING HEARING

It was demonstrated that the fenestra pseudorotunda does not represent a secondary homology for archosaurs. However, while it is plausible that it appeared only once in Pseudosuchia (in Crocodylomorpha during the Late Triassic), it also represents a homoplastic character for Dinosauria, appearing seven times independetly. Most of the changes occurred in the Upper and Early Cretaceous (3 each), followed by the Middle Jurassic and Late Triassic (2 each), and by the Upper and Early Jurassic (2 each). Nevertheless, these represent both appearance and losses, and the sub-division of the metotic foramen happened mostly in the Late Triassic and Middle Jurassic (2 each), followed by Middle Triassic, Late Jurassic, and Lower and Late Cretaceous (1 each). There are no appearences in the Early Triassic or Jurassic. In contrast, reversals to the plesiomorphic condition occur mostly in the Upper and Early Cretaceous (2 each), but also in the Early Jurassic (once). Ornithischians and saurischians show an equal number of state changes (6), two of which represent appearences in the former group, while in the latter there were five. This means impedance-matching hearing appeared more times independently in Saurischia, but it was lost more often in Ornithischia. Within Ornithischia, the group with the highest number of changes was Ornithopoda (2), while Ankylosauria and Ceratopsia showed only one change. In Saurischia, Sauropodomorpha shows two acquisitions, while Theropoda shows three, plus one loss – meaning that, of all dinosaurian groups, Theropoda has the greatest plasticity. The first appearance of the character in archosaurian and dinosaurian history, however, happens in Ornithischia in the Middle Triassic.

The connection between the origin of buzzing and stridulating insects with the appearance of the fenestra pseudorotunda was not directly tested, but seems to have little support. First, the origin of clades such as Orthoptera, Coleoptera and Auchenorrhyncha dates from the Carboniferous and Permian (Béthoux *et al*. 2012, Kukalová 1969, Shcherbakov 2002), and the origin of insect flight may be even older, dating from the late Devonian (Gaunt & Miles 2002). Therefore, these events long precede the appearance of the fenestra pseudorotunda not only in any of the clades investigated, but also in all other amniote groups. Likewise, Cicadidae appears in the Eocene (Cooper 1941), postdating the appearences documented. The only group of such insects that has its origin during the Mezosoic is Diptera, whose earliest taxa date from the Middle Triassic (Krzemiński & Krzemińska 2003). The appearance of impedance-matching hearing in Ornithischia takes place at this time, but since herbivory is reconstructed as being plesiomorphic for the group

(Barrett *et al*. 2010), a correlation is not supported. In fact, not only are the origin times of these groups different from the several appearances of impedance-matching hearing (including other amniote groups), but also none of the dietary habits of most, if not all, of the surveyed groups are associated with insectivory. Therefore, other selective forces must be contributing to the evolution of this character. Intraspecific communication might have a more significant role, especially for omnivores or herbivores like ornithischians, since it can act as both a selective force per se and also as a predation pressure. On the other hand, it is not clear which forces would be on play for the loss of impedance-matching hearing since its presence extends the hearing range into higher frequencies, but its absence does not necessarily imply in a better lower extension.

DIVERSIFICATION

CLADE DIVERSIFICATION

Diversity is an important component of macroevolutionary studies that is often loosely defined and applied. It can refer to the diversity of forms exhibited by a given group (currently defined as disparity), or to the number of different species in a given area or ecosystem (richness) or in a given clade (taxonomic diversity). Counting the number of taxa in a clade over time and/or space is a classical approach to diversity estimates, and has been subject of recent methodological refinement when applied to the fossil record as to compensate for geological and anthropogenic sampling biases (Benton *et al*. 2011, Upchurch *et al*. 2011). Diversification events are said to occur when groups either speciate or avoid going extinct in a pattern different from expected in a normal tempo of evolution when compared to their sister clades (Brusatte *et al*. 2010a). Shifts in the diversification rates have been calculated for dinosaurs and for archosaurs as a whole, but they differ from the analysis carried out in the present study. In the study on non-avian dinosaur (Lloyd *et al*. 2008), an extensive supertree was assembled to estimate the shifts for the group only and all valid dinosaur genera in the time was added to it. The archsoaur study (Brusatte *et al*. 2010b), on the other hand, focused on Triassic and Early Jurassic groups only. Because these works were focusing on one aspect of dinosaur and archosaur radiation, diversification, with less strict links to other macroevolutionary measurements such as character changes, the number of taxa covered could be wider. Focusing on braincase data is limiting, as the number of materials available is markedly less abundant than those used for other proxies such as body size and mass estimations – which can rely on many paired and incomplete skeletal elements. The current analysis includes 281 taxa (136 dinosaurs and 144 pseudosuchians), of which 111 could be coded. An alternative supertree with 689 taxa was constructed but since the proportion of informative taxa decreased, results were diluted and a lot more difficult to interpret with confidence. I thus chose to keep a smaller supertree in order to avoid a superficial discussion.

TREE SHAPE ANALYSIS

Phylogenies provide not only hypotheses on the interrelationships of organisms, but also on the temporal distribution of branching events and on the topological distribution of species diversity across its branches. Topological methods for inferring diversification rates compare the difference observed in species diversity between sister-groups to a distribution of the diversity differences generated under a stochastic model, while temporal methods use branch-length estimates to infer the timing of diversification events and compare the observed distribution of branching times to that generated under a null model of random diversification (Chan & Moore 2004). Research on diversification rates has mostly focused

on temporal methods because of the advantage in power provided by incorporating information on the timing of diversification. However, some data types and/or inference methods yield trees that are unsuitable for analysis by temporal methods, such as supertrees or parsimony-based phylogenies. Furthermore, diversification rates may be associated with variables whose estimations are directly or indirectly correlated to branch-length estimates, such as the relationship between rates of diversification and rates of morphological evolution – which is the current case. In these cases, attempts to understand the correlation of the variables to rates of diversification will be confounded if both are conditioned on the same set of branch-length estimates (Chan & Moore 2004).

According to the Yule model, each cladogenetic event results in the appearance of two sister groups, which, if allowed the same amount of time to diversify, will present the same number of resulting clades at any given time. Since this is usually not the case, as some groups show an increased number of taxa when compared to their sister-groups, tree-shape analysis methods compare the postulated diversity of each group to its sister group and to its theoretical capacity of diversification under a Brownian model of evolution. The likelihood of a shift at a given internal branch is based on the likelihood ratio of the observed diversity between in- and outgroups clades and conditioned by the likelihood of a rate shift in the ingroup – which is, in turn, based on the likelihood ratio of the observed diversity between its internal sister-groups. The statistics developed by Moore *et al*. (2004) are based on likelihood ratios of ingroups and were termed Δ_1 and Δ_2.

The first of these takes the difference between likelihood ratios assessed at both a more and a less inclusive node, conditioning the evidence for a shift in the more inclusive node as reflected by the likelihood ratio of a yet more inclusive node, by the evidence of a shift in a less inclusive node, as reflected by the likelihood ratio of diversity of yet less inclusive nodes. The second statistics, on the other hand, attempts to adjust the diversity of less inclusive nodes when calculating its likelihood ratio by excluding the number of species it contains that can be attributed to a rate increase along the branch. In other words, the probability of a rate shift at a branch times the number of species resulting from that shift is subtracted from the total diversity of an anterior branch. For the present tree shape analysis were considered the *P*-values of nodes calculated under the Δ2 shift statistic only.

Shifts in diversification rates were calculated for the assembled phylogeny using the software SymmeTREE v 1.1 (Chan & Moore 2004). The tree topology was exported from Mesquite in Nexus format for detection of diversification rate variation and location of the shifts. Because node numbering system differs between Mesquite and SymmeTREE, results were interpreted with the help of the “ape” (Analyses of Phylogenetics and Evolution – Paradis *et al*. 2004) package for R. Both SymmeTREE and APE count the nodes in a ladderised fashion, although they do not ladderise the topologies themselves. This means

they count terminal taxa first, from left to right (or from top to bottom), and then start counting nodes from the root, which will be number of terminal taxa plus one. At each node, counting continues to the left (or to the top) of the node until it hits a terminal taxon, going back to the most recent node with clades on the right (or below) yet remaining to be counted. Mesquite, on the other hand, has its own system which starts counting nodes by the root (so that the first node is number two) and then numbers nodes or terminal taxa on the left (or top) in order of appearance. As long as the same file exported from Mesquite is used for both SymmeTREE and APE, there should be no problems with node numbering between these two programmes. However, caution is required for other softwares such as PAUP and MacClade. The latter, for instance, automatically rearrange terminal taxa by right-ladderising tree topology, so that the longest clades are always shown on the right side of a given node, and this affects node numbering. One way to avoid this would be to right-ladderise topology before exporting the nexus tree file.

SHIFTS IN DIVERSIFICATION RATES

Having a null hypothesis based on birth-death model that assumes every lineage has an equal, yet independent random probability of speciation in a given time, the diversities of two sister clades are expected to be equivalent. As they usually are not, the probability of how each node deviate from the expected model is assessed. For this analysis, not only statically significant values ($p < 0.05$) were considered, but also marginally significant ones ($0.05 < p < 0.1$). A total of sixteen shifts in the diversification rates were identified in this tree.

The first two shifts occurred outside Archosauria. The first shift happened at node 288 (p=0.0394226) containing *Euparkeria* and its sister-group with the remaining of archosauriform taxa. The second occurred in the following node 289 (p=0.0257077) consisting of Phytosauria + Archosauria. Both of these are Early Triassic in age.

In Pseudosuchia (Figure 29), six shifts occur in total. The first shift was marginally significant (p=0.0790991) and happened at node 314 containing *Batrachotomus* and its sister-clade in the Middle Triassic. The next shift is statically significant and takes place at node 322 (p=0.0403976) consisting of *Almadasuchus* and its sister-group, later in Crocodylomorpha and during the Late Triassic. The following shift is also significant and takes palce at node 339 (p=0.0433622) containing *Hsisosuchus* + Mesoeucrocodylia in the Early Jurassic. Two shifts occur in Notosuchia. The first is significant and takes place at the basalmost node of the clade, on node 343 (p=0.0492063) consisting of taxa from *Anatosuchus* to *Zulmasuchus* in the Early Cretaceous, and a second is highly significant (p=0.010989), in the Late Cretaceous at node 365 at the base of Sebecosuchia. The last shift in the diversification rates of pseudosuchians is also hightly significant (p=0.0157895)

and occurs in the Middle Jurassic, early in Metriorhynchoidea, at the node 400, which includes *Purranisaurus* and the remaining of the taxa.

In Dinosauriformes (Figure 30), the first, highly significant shift happens at its basalmost node, at node 420 (p=0.0174604) consisting of Silesauridae + Dinosauria in the Middle Triassic. In Ornithischia, three shifts were found. The first is also highly significant (p=0.0148148) and takes place at node 424, at the base, comprising *Eocursor* + Gensauria in the Late Triassic. The second shift, however, was marginally significant (p=0.0701754) and occurred at node 427, consisting of *Scelidosaurus* and the remaining of Thyreophoroida in the Early Jurassic. The last shift happened in the Middle Jurassic, at node 444 (p=0.0423387) containing *Hexinlusaurs* + Cerapoda. The last four shifts in the analysis are found in Saurischia, equally divided between Sauropodomorpha and Theropoda. In the first clade, one marginally significant shift (p=0.0768116) happened in the Late Triassic at node 481, in the origin of Massopoda, while the other was found in the Early Jurassic at node 493 comprising *Jobaria* + Neosauropoda (p=0.025641). The last two shifts were marginally significant. One occurred at node 509 (p=0.0626642) including *D. wetherelli* and the remaining of neotheropods, and the other at the node 515 (p=0.0504202) containing *Monolophosaurus* + Tetanurae – both in the Late Triassic.

Discussion: These results contrast with the ones published for Archosauria (Brusatte *et al*. 2010b) in which no significant shifts were found on this side of the tree. The difference in results could be attributed to the limited taxon sampling of crocodylomorphs, since the analysis is limited to the Trissic and Early Jurassic, but to confirm that further tests are needed. Many diversification studies partition the timescale (bins) in order to follow the variation of the rate shifts through time, and also because when dealing with a time-unconstrained phylogeny, results may not be comparable. Although this phylogeny is both clade- and time-constrained, as are most of other fossil-based phylogenies whose terminal taxa often exhibits one or more groups that persist past the time-spam analysed, binning analyses were not performed here as I was not interested in the shifts variations throughout the Mesozoic. If one clade is allowed more time to diversify, however, then it will likely show higher rates at the base of the group and thus the results may differ. Therefore, allowing a longer time-spam for pseudosuchians, shifts can be identified at the base of more inclusive clades – and this may be the reason why the results differ. One of the clades does persist past the Mesozoic and into the Paleogene (Sebecidae), but since it has likely origins in the Late Cretaceous as implied by ghost lineages, they were not removed from the analysis – if it is excluded, the second shift within Notosuchia disappears and some p values alter slightly, but only marginally. It is also interesting to notice that both diversification events have been suggested (Pol *et al*. 2014). Nonetheless, the results for Arhcosauria as a whole, where the

majority of the shifts (7 out of 14) take place in the Triassic, also agree with indications of early and intense diversification events in archosaurs, supporting an adaptive radiation hypothesis (Brusatte *et al*. 2008a, Brusatte *et al*. 2010a, 2010b).

Although no significant shift was found for pseudosuchians in Brusatte *et al*. (2010b), results found here are compatible with the raw diversity counts presented therein, where increases in the Late Triassic and Early Jurassic were identified. To date, no other published study has considered such a broad coverage of pseudosuchians, although an analysis currently in progress by Bronzati *et al*. has found similar results, albeit being restricted to Crocodylomorpha only. Pseudosuchian clades showing significant shifts in their diversification rates appeared somewhat early in their evolutionary history. Of the five clades identified, four appear almost in sequence: Middle Triassic, Late Triassic, Early Jurassic and Middle Jurassic. The last, however, originates only in the Early Cretaceous and is directly correlated with the radiation of notosuchians (see below).

A peak in diversity of non-dinosaur dinosauromorphs occurred in the Middle Triassic (Irmis 2010) and a diversification shift is also identified here. The first study on diversification rates of dinosaurs found a total of 26 significant and marginally significant shifts (Lloyd *et al*. 2008). The differences, as mentioned before, are likely due to taxa coverage, which was much more extensive in the cited study. Although taxon sampling and phylogenetic relationships vary, some similarities were found. In ornithischians, shifts in the cited study occur in Genasauria (LT), Eurypoda (EJ), and Cerapoda (LT), which in the current tree are equivalent to the Gensauria, Thyreophoroida and Cerapoda nodes. However, the shift in Cerapoda is identified here as occurring in the Middle Jurassic, due to our updated phylogeny. Although ornithischians are very scarce in the fossil record during the Late Triassic, residual (sampling corrected) diversity estimates indicate a peak for the clade during this time (Upchurch *et al*. 2011). An increase in diversity in the Early Jurassic was also identified (Irmis 2010), and has been linked to niche occupation (Butler *et al*. 2007). During the Middle Jurassic, ornithischian diversity begins to increase again (Upchurch *et al*. 2011). This trend closely matches the ones identified here for the group.

The basal relationships of saurischians have undergone significant transformations in the recent past, and have affected the phylogeny of both sauropodomorphs and theropods, so that a correlation with the current results is less direct. In Lloyd *et al*. (2008), the phylogenetic relationships of basal sauropodomorphs are strinkingly different from those presented here, and thus a comparison is more difficult. Two shifts were identified at the base of Sauropodomorpha in the Middle Jurassic, plus one in a Plateosauridae + Massospondylidae clade. These likely are correlated to the Massopoda shift found here in the Late Triassic. A shift is also identified by Lloyd et al. at around Neosauropoda in the Early Jurassic, corresponding to our neosauropod shift in the same period. A peak in the diversity

of sauropodomorphs in the Late Triassic is well estabilished in the literature (Barrett *et al*. 2009, Brusatte *et al*. 2008a, Mannion *et al*. 2011, Upchurch *et al*. 2011), and has been hypothesised as an opportunistic radiation after the extinction of non-dinosaurian herbivores in the early in the epoch. On the other hand, the Triassic-Jurassic boundary seems to have little effect on sauropodomorph diversity, with estimates being similar to those of the Late Triassic (Irmis 2010, Upchurch *et al*. 2011). This contrasts with our analysis and with Lloyd *et al*. (2008), in which shifts for the time were found in Neosauropoda. Within theropods, Lloyd *et al*. (2008) find several shifts throughout the tree, but the one just after the branching off of Coelophysoidea and the one just on its base in the Middle Triassic should correspond to that found in Neotheropoda in the Late Triassic in our study. Also in the Late Triassic, two other very closely occurring shifts in Tetanurae and Avetheropoda should correspond to the Tetanurae shift found here. Irmis (2010) also identifies a peak in diversity in the Late Triassic, but attribute it to herrerasaurs. Increases in Late Triassic diversity of theropods are not as marked as for sauropodomorphs, but a trend exists and is compatible with the data here (Upchurch *et al*. 2011). On the other hand, the analysis of Benson *et al*. (2013) retrieved no significant diversification shifts for non-pygostylian theropods and the reasons for this are completely obscure: taxa sampling of non-maniraptorans at the base of tree seems extensive and equivalent to thatshown here. As they considered only the significant shifts and ignored the marginally significant ones, this could partially explain the results.

With six of the seven dinosaurian shifts found occurring in the Late Triassic and Early Jurassic, they confirm the hypothesis that intense diversification events took place early in the evolutionary history of dinosaurs. However, it contrasts in some points with Brusatte *et al*. (2008b) and Irmis (2010). The latter finds no changes in clade origination rates either in the Late Triassic or in the Early Jurassic, while we find a total of 6 shifts in the time. Also, the former found more significant increases in dinosaur diversity in the Early Jurassic. Our results show that the Late Triassic was more important for the group with four shifts – and for theropods in particular, showing two of them. In fact, a decrease in diversity is found later in the Early Jurassic for the group, but this could be due to biases (Irmis 2010:402). It should be noted here that Lloyd *et al*. (2008:2486) states that two significant and two marginally significant shifts occur in the Triassic, while in the Jurassic there are 11 and 7, respectively. However, when the shifts for the individual bins are counted, the correct amounts should be 9 and 4 for the Triassic and 4 and 5 for the Jurassic. This difference between data set and text is probably because the bins 2 (Carnian) and 3 (Norian) were mistakenly considered as belonging to the Jurassic (Lloyd pers. comm.). Therefore, the statement that “quantitative analysis of diversification have identified the Early Jurassic as the single most important time period for lineage diversification” in dinsoaurs must be taken with caution (Brusatte *et al*. 2008b:734). A peak does occur in the mean values of Δ_2 shifts in the Early Jurassic, but this

only means that the shifts were statistically more significant, not necessarily that they were more important or abundant. Although the bins do not exactly coincide with the epoch and stage divisions, the time with the highest number of shifts is the Late Triassic, with 9 shifts in total – followed by the Early Jurassic with 5.

TRAIT DIVERSIFICATION

Several evolutionary theories postulate a relationship between species diversification and morphological divergence of clades. The adaptive radiation theory predicts high rates of speciation triggered by adaptive morphological divergence, while the hypothesis of punctuated equilibrium predicts morphological divergence occurs at speciation events, resulting in a positive correlation between diversification and phenotypic divergence rates (Adams *et al*. 2009, Brusatte 2011, Llyod *et al*. 2011, Silvestro *et al*. 2013). The identification of factors that may drive the differentiated diversification among clades has included biogeography, climate change and the evolution of key innovations (Llyod *et al*. 2011, Silvestro *et al*. 2013). While it has been demonstrated that, for some clades, rates of species diversification and morphological evolution are not significantly correlated (Adams *et al*. 2009), key innovations have been positively identified for others (Silvestro *et al*. 2013). As mentioned earlier, although other evolutionary rates have been investigated for archosaurs in general or dinosaurs in particular, the explicit correlation between both or the search for key innovations have not been explored for archosaurs, with the exception of the appearance of herbivory in dinosaurs (Barrett *et al*. 2010). In this, the reconstruction of the ancestral mode of dinosaur diet could not recover any as the plesiomorphic state for dinosaurs. When dinosaur clades were separated, herbivory/omnivory was recovered for ornithischians and sauropodomorphs, but only in the latter group was a correlation with diversity found. The aim of this section is, therefore, to try to correlate the shifts in diversification rates with other calculated rates in archosaur and dinosaur evolution and with the appearance of potential key braincase innovations, in particular of impedance matching hearing.

METHODS

Methods correlating rates of morphological evolution with diversification rates are only recently being applied in case studies and associations between character evolution and shifts in rates of diversification are made based on tree topology.

Character-Associated Diversification: The association between rates of diversification and character evolution is a recent and fast-expanding methodological field in studies of macroevolution (Davis *et al*. 2013). One of these methods is the BiSSE (Binary State of Speciation and Extinction – Maddison *et al*. 2007). There are, however, a few limitations with this method that only recently have been addressed. For instance, it only recognises binary-state characters, whereas our matrix contains multiple-state characters as well. Furthermore, it can only be applied to completely resolved phylogenies. Branch-lengths and altimetric topology may or may not be further issues. In this sense, the R package "diversitree" (comparative phylogenetic analyses of diversification – FitzJohn 2012) seems to be the adequate solution, as it implements several of these methods. However, due to time issues, these were not applied here, but are being considered for publication.

Evolutionary Rates

In recent years, dinosaurs have experienced a growing number of studies concerning the patterns of their early radiation and diversification, mostly due to the development of new analytical methods. While only a few have been concerned to their taxic diversification, as explored in the previous section, many have focused on the evolution of certain traits, such as limb length and, in particular, body size (Benson *et al*. 2014, Brusatte *et al*. 2012, Dececchi & Larsson 2013, Puttick *et al*. 2014). However, very few studies have attempted to correlate disparity or trait evolution patterns with diversification (Barrett *et al*. 2010, Brusatte *et al*. 2010b). I am aware it is difficult to compare the results obtained here with other published diversity studies because of varying taxa sampling and phylogenetic relationships considered, but it is still worth comparing them with the available data before surveying correlations between the shifts and the character changes of the previous chapter.

Pseudosuchian body, cranial, mandibular and biomechanic disparity has been shown to be high in the Late Triassic (Brusatte *et al*. 2008a, Stubbs *et al*. 2013, Toljagić & Butler 2013). Although the clade suffered major taxic losses in the Triassic-Jurassic boundary, with the extinction of all non-crocodylomorph clades, cranial disparity was rapidly recovered in the Early Jurassic and remained basically unchanged through the boundary (Toljagić & Butler 2013). The increase in crocodylomorph disparity matches the diversification shift found for the epoch. Mandibular morphological variation increased considerably in the Cretaceous during the radiation of notosuchians (Stubbs *et al*. 2013) and this is also compatible with the shift found here. On the other hand, low disparity was found for thalattosuchians in the Jurassic (Stubbs *et al*. 2013), while here a significant shift was identified. Pseudosuchian maximum body sizes increase in the Lower and Middle Triassic, becomes stable in the Late Triassic and decreases just prior to, and into the Triassic-Jurassic boundary (Turner & Nesbitt 2013). The shift in the Middle Triassic could be correlated with body size increase,

but more interestingly, the drop in body size in the later Late Triassic is mostly correlated with crocodylomorphs, just as the shift found here prior to the origin of Crocodyliformes. Therefore, it could be that high diversification rates are correlated with increases in body size in the Middle Triassic, with high body disparity but a drop in body size in the Late Triassic, with cranial disparity in the Early Jurassic, and with jaw disparity in the Early Cretaceous, although a cause and effect relationship may be more difficult to identify. On the other hand, the thalattosuchian shift in the Middle Jurassic seems not to be correlated with any metrics, and thus other factors might be triggering, or being driven by, these radiation events.

Dinosaurian evolutionary rates of skeletal character changes were significantly high in the Middle Triassic, but show a decrease in the Late Triassic. On the other hand, they present a major trend of increase in disparity, with a significant peak before the Triassic-Jurassic boundary, then remaining essentially constant after it, but with a small peak in the Early Jurassic (Brusatte *et al*. 2008a, 2008b, 2010a, 2010b). In our analysis, these different peaks occur at the same time as five of the shifts in diversification rates: one in the Middle and the others in the Late Triassic. When considering the disparity later in the history of the group, sauropods exhibit a slight increase in the later Late Cretaceous, while ceratopsids and hadrosaurids show a decrease, but only the latter is non-significant (Brusatte 2012). No shifts were found here within any of these groups in the given period, although Lloyd *et al*. (2008) do identify a shift for ceratopsids at the time, only slightly earlier. Dinosaur body size increased in the Late Triassic and in the Early Jurassic, but the increases are not significantly different from each other (Irmis 2010, Turner & Nesbitt 2013). Sauropodomorphs were responsible for this trend, although theropods also show an increase in maximum body size at the end of the Triassic. Shifts in both groups occur at the time, two in the latter and one in the former. Among ornithischians, body size increase is identified only in thyreophorans in the Early Jurassic, and a shift in diversification rates do occur in the group at the time. On the other hand, a more refined analysis by Benson *et al*. (2014) identified 23 significant shifts in the rates of body size evolution of dinosaurs. While it is difficult to temporally correlate these shifts in rates of morphological evolution with the diversification shifts found herein, due to a lack of refinement in the division of the timescale, a phylogenetic comparison is easier. The coincident shifts present in both analyses are found in Thyreophora and Tetanurae only – although the latter is regarded as happened in the Jurassic, in contrast to the Late Triassic age calculated here.

BRAINCASE CHARACTER CHANGES

It is also possible to correlate the state changes in the braincase characters surveyed with the shifts in diversification rates found (Table 2*). When analysed with parsimony however, only a limited number of changes could be associated with diversification shifts with

certainty. In Pseudosuchia, the diversification shift in *Batrachotomus* + other Loricata was associated with only two possible changes (character 1: 1 → 0, character 9: 1 → 0 – Figures 33 and 53); that in *Almadasuchus* + Crocodyliformes was associated with one unambiguous change (character 7: 0 → 1 – Figure 46) and three possible changes (character 9: 1 → 0, character 13: 0 → 1, character 15: 1 → 2 – Figures 53, 63, and 68); the shift in *Hsisosuchus* + Mesoeucrocodylia is associated with two possible state changes (character 9: 1 → 0, character 13: 0 → 1 – Figures 53 and 63); that in *Anatosuchus* + other Notosuchia was associated with four possible changes (character 5: 0 → 1, character 9: 1 → 0, character 13 0 → 1, character 15: 2 → 1 – Figures 42, 53, 63, and 68); that in *Gondwanasuchus* + the remaining of notosuchians was associated with four possible changes (character 5: 0 → 1, character 9: 1 → 0, character 13: 0 → 1, character 15: 2 → 1 – Figures 42, 53, 63, and 68); and the last shift in *Purranisaurus* + other Metriorhynchidae was associated with three possible changes (character 9: 1 → 0, character 12: 0 → 1, character 13: 0 → 1 – Figures 53, 61, and 63). These results mean a total of 19 character state changes associtated with 6 shifts in diversification rates, of which change in character 9 (presence of the orbitocerebral vein foramen – Figure 53) was the most common correlation found, being associated with all shifts, followed by character 13 (confluence of the vidian canals – Figure 63), associated with five shifts and character 15 (level of the pneumatisation of the braincase – Figure 68) with three shifts. It is worth noting that the first two characters are possibly associated with the majority of the shifts because the ancestral state could not be reconstructed for most of the topology in this part of the tree, and therefore this correlation is very weak. The same holds true for character 15 (Figure 68) and Notosuchia. On the other hand, it is interesting to notice that the one character that was associated with certainty with one diversification shift was the presence of the fenestra pseudorotunda (character 7, in Crocodyliformes – Figure 46).

Because parsimony analysis can only reconstruct the ancestral states in an all-or-nothing manner, and therefore, in theory, uncertainties mean a 50-50 chance of each state being true for a certain branch, I used the likelihood method to calculate the probability of a change occurring in a given branch. The shift in *Batrachotomus* + other Loricata was associated with three character changes (character 9: 1 → 0 [100] – Figure 78[*]), character 11: 0 → 2 [99.92], character 14: 0 → 1 [69.07] – Figures 80 and 81); that in *Almadasuchus* + Crocodyliformes was associated with four (character 1: 0 → 1 [66.78], character 7: 0 → 1 [99.32], character 8: 0 → 1 [98.37], character 16: 0 → 1 [95.06] – Figures 74, 76, 77, and 83);

[*] Please note that Table 2 and figures corresponding to the results of the ancestral state reconstruction by likelihood are to be found at the end of this chapter. Figure order follows character numbers, with pseudosuchian results shown first, then dinosaurian.

that in *Hsisosuchus* + Mesoeucrocodylia was associated with eight (character 1: 0 → 1 [52.11], character 3: 0 → 1 [99.15], character 7: 0 → 1 [99.92], character 8: 0 → 1 [82.04], character 10: 0 → 1 [99.99], character 11: 0 → 2 [98.75], character 15: 0 → 1 [96.28], character 16: 0 → 1 [99.99] – Figures 74, 75, 76, 77, 79, 80, 82, and 83); that in *Anatosuchus* + other Notosuchia was associated with five (character 1: 1 → 0 [86.32], character 3: 1 → 0 [100], character 10: 0 → 1 [99.99], character 11: 0 → 2 [81.90], character 15: 1 → 0 [100] – Figures 74, 75, 79, 80, and 82); that in *Gondwanasuchus* + the remaining of notosuchians had no associated changes, and that in *Purranisaurus* + other Metriorhynchidae was associated with two (character 7: 0 → 1 [99.94], character 16: 0 → 1 [95.07] – Figures 76 and 83). This makes a total of 22 likely state changes in correlation with five shifts in diversification rates. By far the shift with the highest amount of changes was the one in Mesoeucrocodylia. Among the characters associated with this node, are the ones more often associated with other pseudosuchian shifts: character 1 (orientation of the paroccipital process – Figure 74), character 7 (presence of the fenestra pseudorotunda – Figure 76), character 11 (ossification of the anterior braincase wall – Figure 80), and character 16 (enclosure of the Eustachian tubes – Figure 83) with three correlations each. In this likelihood analysis, the majority of the characters are highly homoplastic, appearing several times independently for almost every taxon scored – this is for instance the case with the fenestra pseudorotunda.

For Dinosauria, in general more character state changes were found to be associated with shifts in diversification rates for both analyses. In the parsimony analysis, the shift in Silesauridae + Dinosauria was associated with two possible changes (character 2: 1 → 0, character 10: 1 → 0 – Figures 36 and 57). In Ornithischia, the shift in *Eocursor* + Genasauria had three possible associated character changes (character 2: 1 → 0, character 10: 1 → 0, character 11: 0 → 1 – Figures 36, 57, and 60), that in *Scelidosaurus* + other Thyreophoroida had one unambiguous associated change (character 2: 1 → 0 – Figure 36) and three other possible associated changes (character 1: 1 → 0, character 7: 1 → 0, character 10: 1 → 0, character 11: 0 → 1 – Figures 36, 47, 57, and 60), and that in *Hexinlusaurs* + Cerapoda had three associated changes (character 2: 1 → 0, character 11: 0 → 1, character 14: 0 → 1 – Figures 36, 60, and 66). In Sauropodomorpha, the shift in *Riojasaurus* + other Massopoda was associated with only one possible change (character 2: 1 → 0 – Figure 36) and that in *Jobaria* + Neosauropoda was associated with five (character 1: 1 → 0, character 2: 1 → 0, character 9: 1 → 0, character 12: 2 → 0, character 14: 1 → 0 – Figures 34, 36, 54, 62, and 66). In Theropoda, the shift of *D. wetherelli* + other Neotheropoda was associated with three possible changes (character 2: 1 → 0, character 11: 0 → 1, character 15: 0 → 1 – Figures 36, 60, and 69) and that of *Monolophosaurus* + Tetanurae was associated with only one

possible character change (character 2: 1 → 0 – Figure 36). In this scenario, diversification shifts in ornithischians are associated with more character changes (11) while those of saurischians with slightly less (10 in total, six for sauropodomorphs and four for theropods). It is also in the former group that the only unambiguous change occurs, in character 2 (anatomy of the CN II foramen – Figure 36) in Thyreophoroida. This is the character with the highest number of associations with shifts, being associated with all of them, followed by character 11 (ossification of the anterior braincase wall – Figure 60) with four associations (three in ornithischians and one in theropods). Once again, like in pseudosuchians, characters 2 and 11 are associated with the majority of the shifts because the ancestral states are highly unresolved in the topology. The presence of the fenestra pseudorotunda (Figure 47) is possibly associated with only one shift, in Thyreophoroida.

The results found with the likelihood analysis were also more abundant for dinosaurs, but in this case significantly higher. At the base of the group, the shift was associated with four changes (character 2: 0 → 1 [66.30], character 3: 0 → 1 [97.71], character 9: 0 → 1 [50.00], character 11: 2 → 0 [68.99] – Figures 85, 86, 89, and 90). In Ornithischia, the shift in *Eocursor* + Genasauria was associated with nine character changes (character 1: 0 → 1 [72.24], character 2: 0 → 1 [71.01], character 3: 0 → 1 [96.84], character 7: 0 → 1 [92.65], character 8: 0 → 1 [98.37], character 9: 0 → 1 [50.00], character 11: 0 → 2 [68.36], character 14: 0 → 1 [79.41], character 17: 0 → 1 [99.89] – Figures 84 – 91, and 93); that in *Scelidosaurus* + other Thyreophoroida was associated with seven changes (character 2: 0 → 1 [92.18], character 3: 0 → 1 [92.00], character 7: 1 → 0 [92.87], character 8: 0 → 1 [98.69], character 9: 0 → 1 [51.00], character 11: 0 → 2 [97.55], character 14: 0 → 1 [94.44] – Figures 85 – 91), and that in *Hexinlusaurs* + Cerapoda was also associated with seven changes (character 1: 0 → 1 [83.28], character 2: 0 → 1 [50.46], character 3: 0 → 1 [97.69], character 7: 0 → 1 [98.68], character 8: 0 → 1 [97.31], character 11: 0 → 2 [67.94], character 17: 0 →1 [99.90] – Figures 84 – 88, 90, and 93). In Sauropodomorpha, the shift in *Riojasaurus* + other Massopoda was again associated with seven changes (character 1: 0 → 1 [89.32], character 2: 1 → 0 [100], character 3: 1 → 0 [100], character 8: 0 → 1 [99.08], character 9: 0 → 1 [51], character 14: 0 → 1 [85.91], character 17: 0 → 1 [99.91] – Figures 84 – 86, 88, 89, 91, and 93), as was the shift in *Jobaria* + Neosauropoda (character 1: 0 → 1 [59.47], character 2: 0 → 1 [60.04], character 3: 0 → 1 [97.38], character 8: 0 → 1 [96.32], character 9: 0 → 1 [50.00], character 11: 0 → 2 [85.19], character 17: 0 → 1 [99.81] – Figures 84 – 86, 88 – 90, and 93). In Theropoda, the shift in *D. wetherelli* + other Neotheropoda was associated with a total of 9 changes (character 1: 0 → 1 [96.52], character 2: 0 → 1 [62.10], character 3: 0 → 1 [91.92], character 8: 0 → 1 [68.83], character 9: 0 → 1 [50.00], character 11: 0 → 2 [94.50], character 14: 0 → 1 [83.60], character 15: 0 →

1 [94.66], character 17: 0 → 1 [99.86] – Figures 84 – 86, 88 – 91, and 93) and that in *Monolophosaurus* + Tetanurae was associated with eight (character 1: 0 → 1 [96.97], character 3: 0 → 1 [92.48], character 8: 0 → 1 [79.72], character 9: 0 → 1 [51.00], character 11: 0 → 2 [99.50], character 14: 0 → 1 [84.80], character 15: 0 → 1 [98.50], character 17: 0 → 1 [99.50] – Figures 84, 86, 88 – 93). In this second analysis, diversification shifts in saurischians are associated with more character changes (31 in total, 14 in Sauropodomorpha and 17 in Theropoda), while in Ornithischia a total of 23 changes are associated with shifts in diversification rates. The highest number of associations with shifts are found in character 3 (anatomy of the CN II and CN IV foramina – Figure 86) and character 8 (number of CN XII foramina – Figure 88), each associated with all the shifts. These are followed by character 1 (orientation of paroccipital process – Figure 84), character 2 (anatomy of the CN II foramen – Figure 85), character 9 (presence of the orbitocerebral vein foramen – Figure 89), character 11 (ossification of the anterior braincase wall – Figure 90), and character 17 (location of carotid canals – Figure 93), with 6 associations each. Although the presence of the fenestra pseudorotunda (Figure 87) is not listed as one of the characters with a significant amount of correlation with shifts, it is interesting to notice that all three times it appears associated with them are in ornithischian shifts.

ARCHOSAUR DIVERSIFICATION

The results found in this analysis are compatible with an adaptive radiation scenario for archosaurs, wherein half of the shifts in diversification rates take place early in their history during the Middle and Late Triassic. When considering the phylogeny only, it is possible to notice that most of these exceptionally diverse groups are more inclusive clades (such as Crocodyliformes, Genasauria and Tetanurae) that have their origin early also in archosaur phylogeny, and not only early in time. This is a trend driven mainly by dinosaurs, as in Pseudosuchia only one-third of the shifts occur in these conditions; the shifts in Pseudosuchia are temporally and phylogenetically well distributed. Three of them are placed in the main crocodilian lineage, whereas two occur in Notosuchia, thus emphasizing the importance of the group for crocodyliform diversity during the end of the Mesozoic and confirming previously suggested radiation events (Pol *et al*. 2014). The diversification shift found in Metriorhynchidae confirms that thalattosuchians were responsible for a good part of Jurassic pseudosuchian diversity, albeit not happening early in the history of the group. In Dinosauria, almost two-thirds of the shifts occur in the Triassic and at the base of its main groups. The same is true for theropods and this is in agreement with recent studies demonstrating that clade diversification is decoupled from the origin of flight, as shifts happen

well before and well after the origin of Avialae. Thus, powered flight possibly cannot be regarded as a key innovation for the group. Also, one shift within Sauropodomorpha occurs later in the phylogeny of the group, contrasting with the general trend of early shifts and resembling the pattern found in pseudosuchians. The shifts in general are fairly well distributed among dinosaur clades, but in contrast to pseudosuchians, it is possible to notice that the majority of the shifts occurred outside the main avialan line. In contrast to ornithischians, whose shifts occurred at the base of its two main clades, the shifts of sauropodormorphs and theropods take place essentially in their main lineage, with no outstanding participation of particular groups. While this may represent a taxon sampling bias for theropods, for which Ceratosauria and Megalosauria may be under-represented, this is likely not the case for sauropods.

Many of the shifts found here are associated with other published metrics of diversity, indicating a multi-facetted diversification event for archosaurs. The few disparity and body size studies available for pseudosuchians find peaks or significant increases at the same times as the shifts, suggesting a possible correlation between taxic and morphological diversification events, the exception being the metriorhynchid shift in the Middle Jurassic. As this particular shift is not correlated with high mandibular disparity and the low number of character changes found in the current study, the causes underlying or being driven by this diversification event are still unclear. The notosuchian shifts, on the other hand, are both connected to an increase in morphological disparity and with character state changes, in particular the shift in the node at the base of the group. One particularly interesting correlation is the Late Triassic shift in Crocodyliformes and the increase in body size found just prior to the Triassic-Jurassic boundary for crododylomorphs by Turner & Nesbitt (2013). This is also one of the shifts with the highest number of associated character changes found here, indicating a close relationship between phylogenetic and morphological diversification. The rate shift occurring in Mesoeucrocodylia seems to be correlated with cranial disparity only and the conflicting results between the parsimony and the likelihood analyses are intriguing: by one method it is only correlated with two changes and by the other, with eight, the highest number of correlated state changes in Pseudosuchia. The shifts found in Notosuchia during the Cretaceous are in agreement with the morphological variation found by Stubbs *et al*. (2013). The group is well-known for its high morphological and ecological diversity, and for the first time it has been demonstrated that it is correlated with taxic diversification as well.

Dinosaurian shifts are also usually correlated with other trends of morphological diversity, namely evolutionary rates of skeletal character changes, disparity and, especially, body size – shifts in the diversification rates of thyreophorans, sauropodomorphs, theropods in general, and tetanurans in particular coincide with increases in their maximum body size.

The most important diversification shifts in terms of number of braincase character changes associated are those in Thyreophroida and Neosauropoda, both occurring in the Early Jurassic. These shifts are usually overlooked in comparison to theropod diversification rates and may indicate that important morphological changes were taking place in the braincase of these groups. In fact, the high number of shifts in ornithischians and the elevated correlation with state changes may suggest that the evolution of this group has been largely ignored in the literature. Due to a lack of broader studies, which have so far focused only in the first or last stages of dinosaur evolution, shifts taking place in the Jurassic have so far not been correlated with other diversity metrics. Since two-thirds of ornithischian shifts happen during this time, this bias may partially explain why ornithischian trends are often overlooked. The shifts of Ornithischia are well distributed in time, occurring in sequence from the Late Triassic to the Middle Jurassic. The correlations with character state changes, however, do not follow the same pattern, as the second shift represents the one with most associated changes in braincase morphology. For the two clades of Saurischia, the trend is reversed: in Sauropodomorpha, the first shift is associated with only one character correlation, while the second is associated with five, while in Theropoda the first shift has three character changes associated with it and the second only one. It seems, therefore, that changes occurring in the braincase morphology played some role early in the diversification rates of theropods but not in sauropods. For the latter group, this indicates that an increase in body size early is not correlated with braincase morphological diversity, contrasting with pseudosuchians. For theropods it is more difficult to discern as shifts occur very close to each other both temporally and phylogenetically.

If, on the one hand, as explored in the previous chapter, character changes were in general constrained by the abutting of the quadrate and pterygoid against the lateral braincase wall on the pseudosuchian side of the tree and thus much less plastic when compared to dinosaurs, on the other these changes were frequently associated with diversification shifts, with a parsimony mean of 3.17 changes per shift for pseudosuchians in contrast to the 2.88 changes for dinosaurs. This could have been a coincidence, where pseudosuchian taxa scored for the present study were associated with important nodes with significant shifts, but only a refinement of the character mapping can solve this. This depends on a better knowledge of crocodiliform braincase anatomy in general. The mean of dinosaurs changes drastically if the likelihood method is considered: pseudosuchians show 3.67 changes per shift and dinosaurs show 7.25 changes per shift. While parsimony reconstructions might have been too vague and are therefore associated with many shifts solely due to uncertainty, likelihood reconstructions may have been too conservative and not represent the true morphological evolution occurring in each group as well – it seems for instance unlikely that the fenestra pseudorotunda is as homoplastic as reconstructed by the

method, especially for pseudosuchians when considering their braincase morphology. The likelihood method was used in an attempt to find more stable correlations between shifts and changes but the characters associated with the shifts vary significantly between both methods, and are usually not the same. It is therefore difficult to combine both results and given the reasons above, it is also difficult to choose one of them in detriment of the other. The difference is likely related to tree size and the corresponding proportion of scored taxa.

IMPEDANCE-MATCHING HEARING

It had been demonstrated in the previous chapter that impedance-matching hearing is not homologous for archosaurs (Figures 46 and 47). With the tree-shape analysis and the identification of the shifts, it can be also concluded that it cannot be regarded as a universal key innovation triggering taxic diversification. Although the ancestral state reconstruction results through parsimony and likelihood are different, and although the braincase of crocodyliforms is still very poorly known in general, it is reasonable to assume that the fenestra pseudorotunda appeared only once in pseudosuchians, given their very peculiar braincase anatomy. It is therefore interesting to notice that one of the shifts in the group is correlated with the sub-division of the metotic foramen. The same is true for ornithischians: although the parsimony and likelihood results are markedly different, a pattern does seem to emerge as the appearance of the fenestra is a recurrent state change in the group, especially in Thyreophoroida. Extant crocodilians are known to be vocal animals, and so were at least one group of ornithischians, thus it is not surprising that a modification of their hearing system is somehow related to their elevated diversification rates. It is, however, unlikely that it is the only factor involved in the diversification of these groups and a multi-factorial and multi-step scenario for these groups seems plausible. In contrast, the appearance of impedance-matching hearing and diversification is completely decoupled in theropods and, although the phylogeny used here does not comprise avialans, they seem also not to be connected in avialans. Impedance-matching hearing does not appear in theropods until later in their phylogeny, while both shifts in their diversification rates take place in the base of the tree. Likewise, in sauropods the impedance-matching hearing seems to have played only a minor role in their evolution and only in certain groups.

Table 2: Summary of correspondences between shifts in diversification rates and character state changes.

Node number	Occurence time	Node name	*p* value	Character number and state change (Parsimony)	Character number, state change and probability (likelihood)
314	MT	*Batrachotomus* + other Loricata	0.0790991	charac1 1-0, charac9 1-0	charac9 1-0 (1), charac11 0-2 (99.92), charac14 0-1 (69.07)
322	LT	*Almadasuchus* + Crocodyliformes	0.0403976	charac7 0-1, charac9 1-0, charac13 0-1, charac15 1-2	charac1 0-1 (66.78), charac7 0-1 (99.32), charac8 0-1 (98.37), charac16 0-1 (95.06)
339	EJ	*Hsisosuchus* + Mesoeucrocodylia	0.0433622	charac9 1-0, charac13 0-1	charac1 0-1 (52.11), charac3 0-1 (99.15), charac7 0-1 (99.92), charac8 0-1 (82.04), charac10 0-1 (99.99), charac11 0-2 (98.75), charac15 0-1 (96.28), charac16 0-1 (99.99)
343	EC	*Anatosuchus* + other Notosuchia	0.0492063	charac5 0-1, charac9 1-0, charac13 0-1, charac15 2-1	charac1 1-0 (86.32), charac3 1-0 (1), charac10 0-1 (99.99), charac11 0-2 (81.90), charac15 1-0 (1)
365	LC	*Gondwanasuchus* to *Zulmasuchus*	0.010989	charac9 1-0, charac5 0-1, charac13 0-1, charac15 2-1	-
400	MJ	*Purranisaurus* + other Metriorhynchidae	0.0157895	charac9 1-0, charac12 0-1, charac13 0-1	charac7 0-1 (99.94), charac16 0-1 (95.07)

420	MT	Silesauridae + Dinosauria	0.0174604	charac2 1-0, charac10 1-0	charac2 0-1 (66.30), charac3 0-1 (97.71), charac9 0-1 (50.00), charac11 2-0 (68.99)
424	LT	*Eocursor* + Genasauria	0.0148148	charac2 1-0, charac10 1-0, charac11 0-1	charac1 0-1 (72.24), charac2 0-1 (71.01), charac3 0-1 (96.84), charac7 0-1 (92.65), charac8 0-1 (98.37), charac9 0-1 (50.00), charac11 0-2 (68.36), charac14 0-1 (79.41), charac17 0-1 (99.89)
427	EJ	*Scelidosaurus* + other Thyreophoroida	0.0701754	charac1 1-0, charac2 1-0, charac7 1-0, charac10 1-0, charac11 0-1	charac2 0-1 (92.18), charac3 0-1 (92.00), charac7 1-0 (92.87), charac8 0-1 (98.69), charac9 0-1 (51.00), charac11 0-2 (97.55), charac14 0-1 (94.44)
444	MJ	*Hexinlusaurs* + Cerapoda	0.0423387	charac2 1-0, charac11 0-1, charac14 0-1	charac1 0-1 (83.28), charac2 0-1 (50.46), charac3 0-1 (97.69), charac7 0-1 (98.68), charac8 0-1 (97.31), charac11 0-2 (67.94), charac17 0-1 (99.90)
481	LT	*Riojasaurus* + other Massopoda	0.0768116	charac2 1-0	charac1 0-1 (89.32), charac2 1-0 (1), charac3 1-0 (1), charac8 0-1 (99.08), charac9 0-1 (51), charac14 0-1 (85.91), charac17 0-1 (99.91)

493	EJ	*Jobaria* + Neosauropoda	0.025641	charac1 1-0, charac2 1-0, charac9 1-0, charac12 2-0, charac14 1-0	charac1 0-1 (59.47), charac2 0-1 (60.04), charac3 0-1 (97.38), charac8 0-1 (96.32), charac9 0-1 (50.00), charac11 0-2 (85.19), charac17 0-1 (99.81)
509	LT	*Dilophosaurus wetherelli* + other Neotheropoda	0.0626642	charac2 1-0, charac11 0-1, charac15 0-1	charac1 0-1 (96.52), charac2 0-1 (62.10), charac3 0-1 (91.92), charac8 0-1 (68.83), charac9 0-1 (50.00), charac11 0-2 (94.50), charac14 0-1 (83.60), charac15 0-1 (94.66), charac17 0-1 (99.86)
515	LT	*Monolophosaurus* + Tetanurae	0.0504202	charac2 1-0	charac1 0-1 (96.97), charac3 0-1 (92.48), charac8 0-1 (79.72), charac9 0-1 (51.00), charac11 0-2 (99.50), charac14 0-1 (84.80), charac15 0-1 (98.50), charac17 0-1 (99.50)

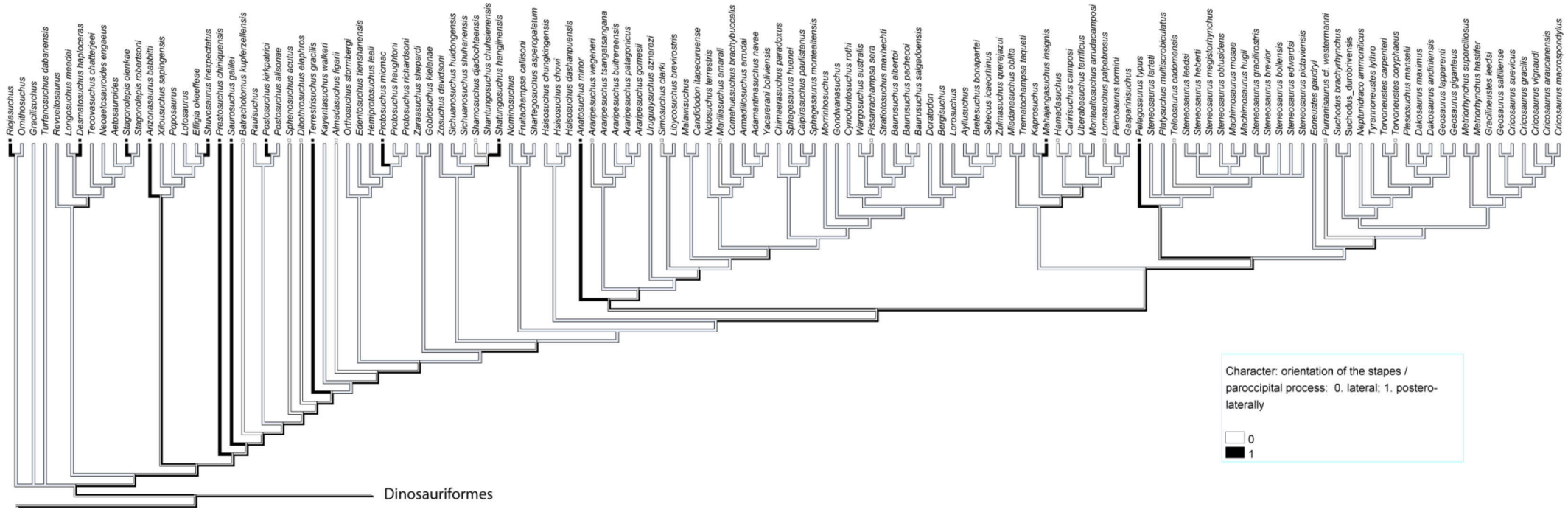

Figure 74: Optimization of character 1 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

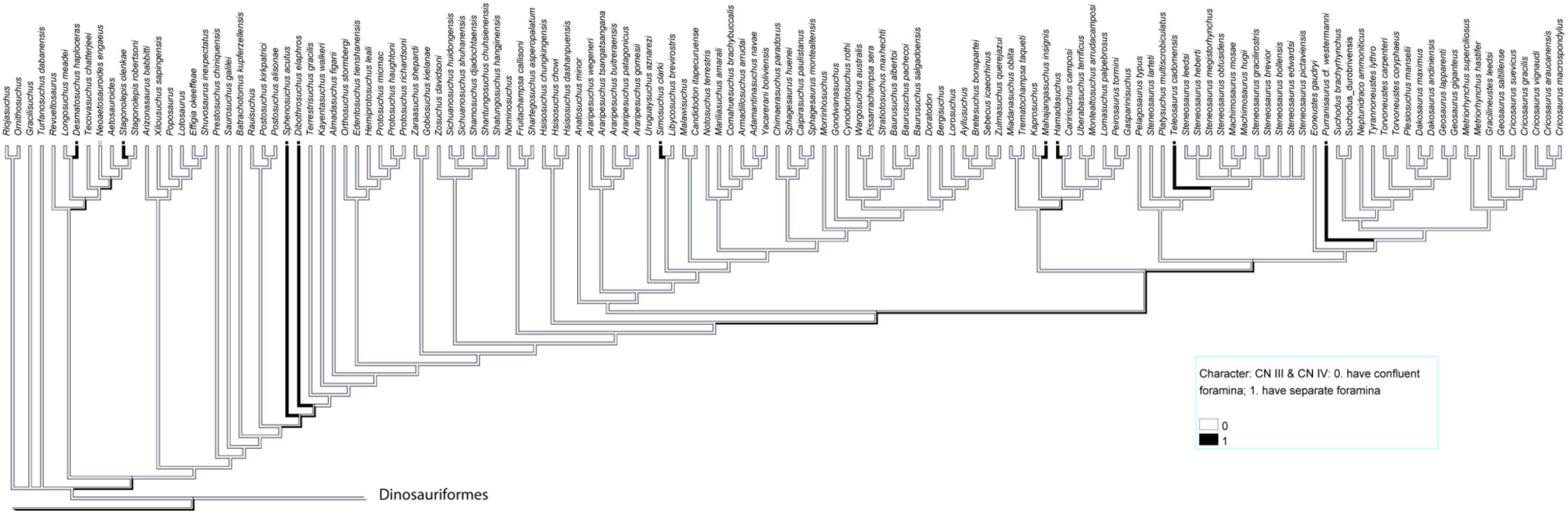

Figure 75: Optimization of character 3 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

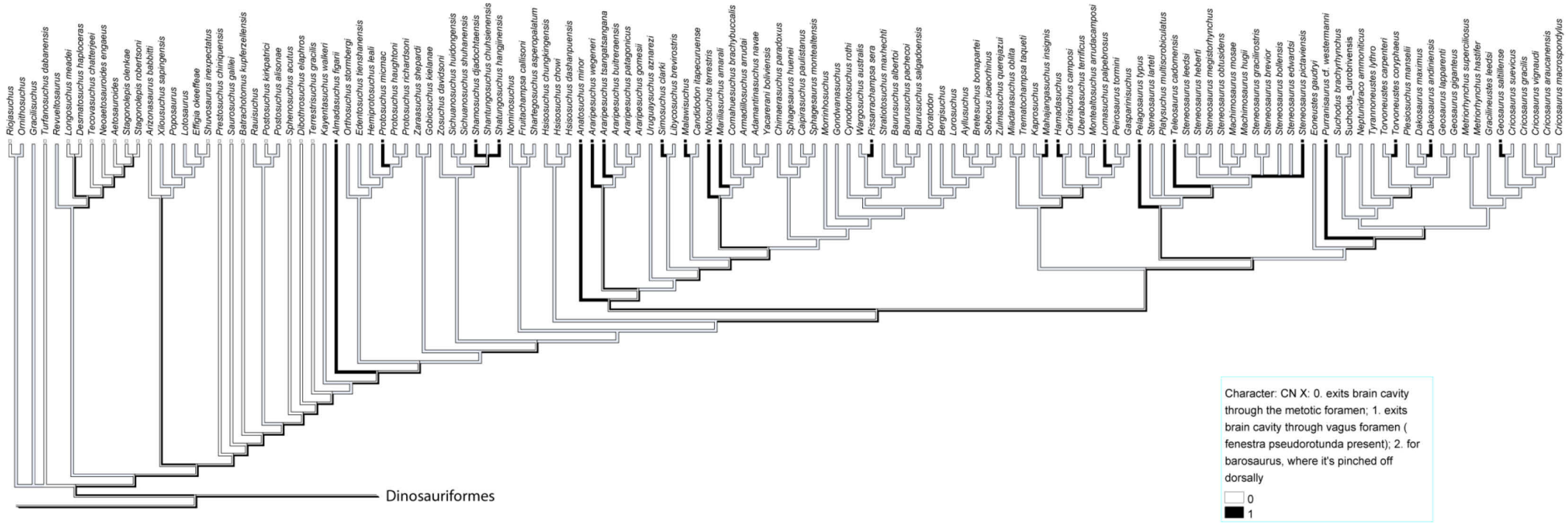

Figure 76: Optimization of character 7 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

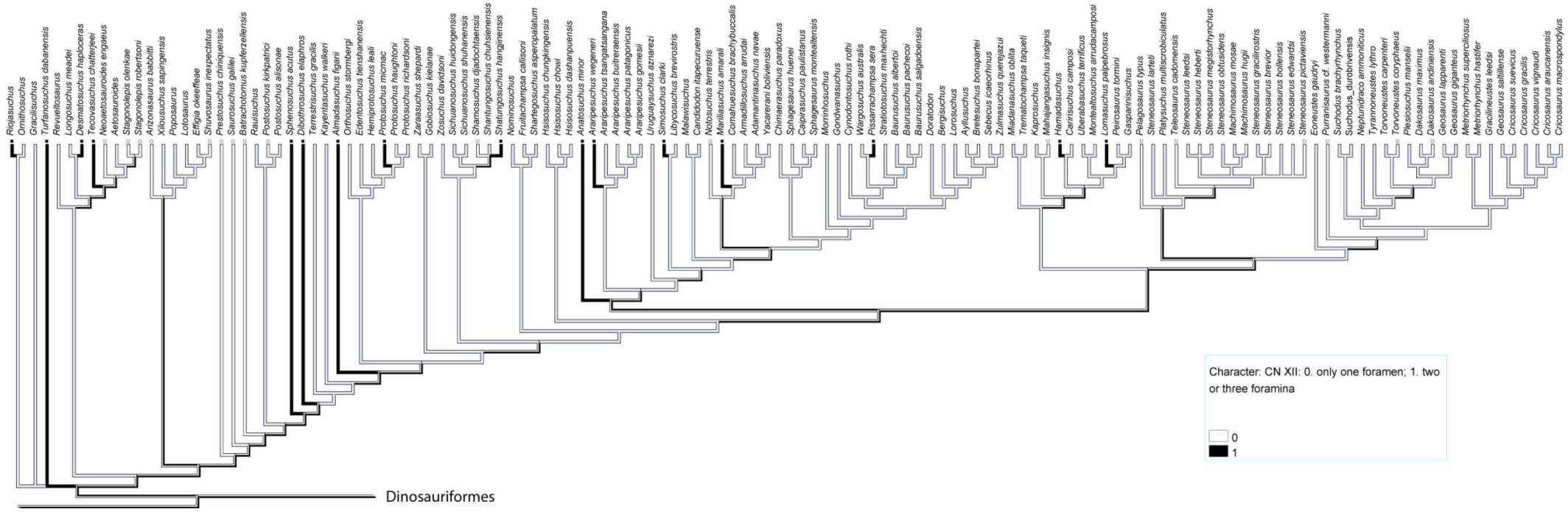

Figure 77: Optimization of character 8 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

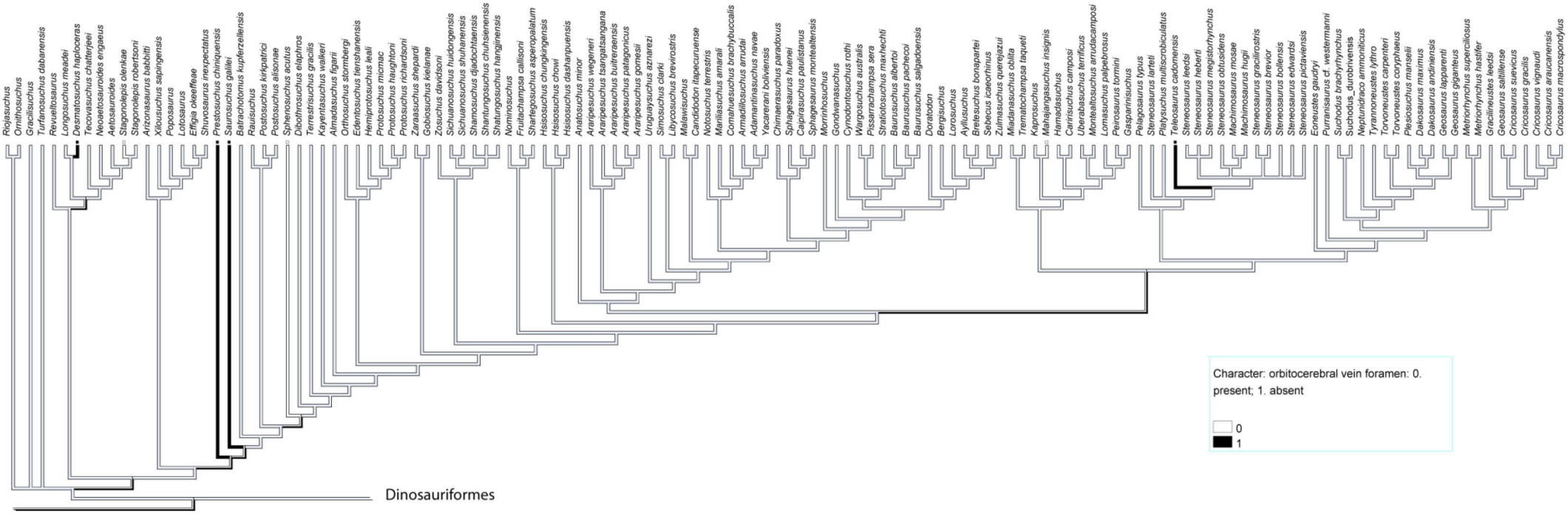

Figure 78: Optimization of character 9 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

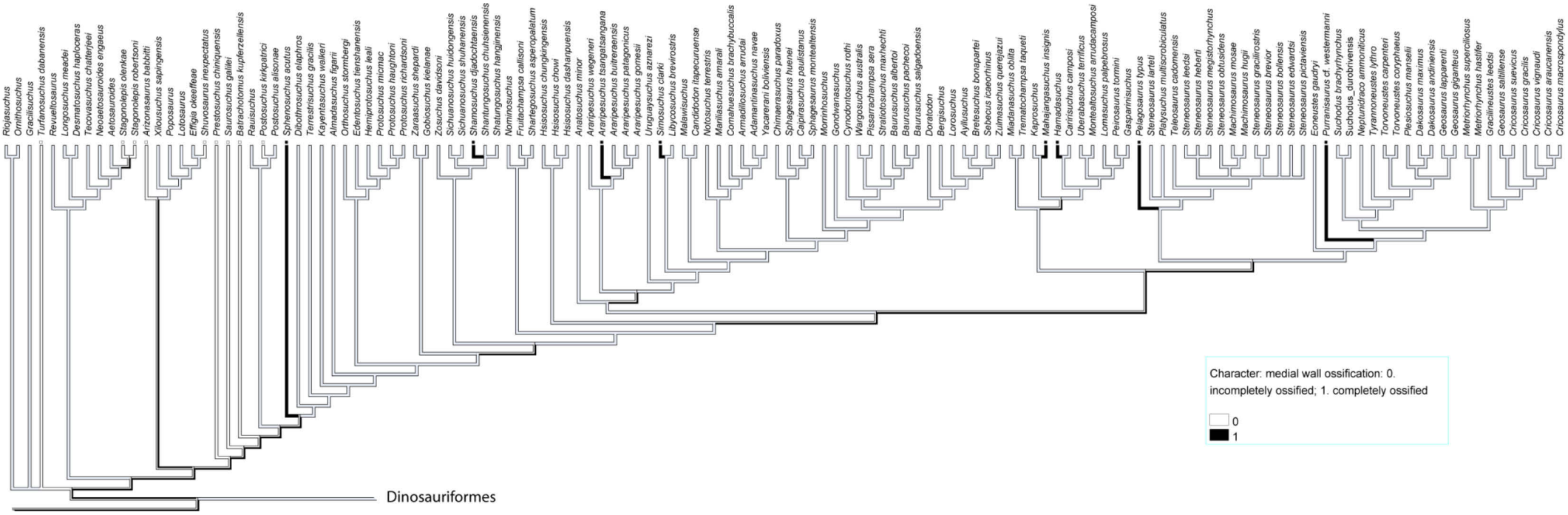

Figure 79: Optimization of character 10 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

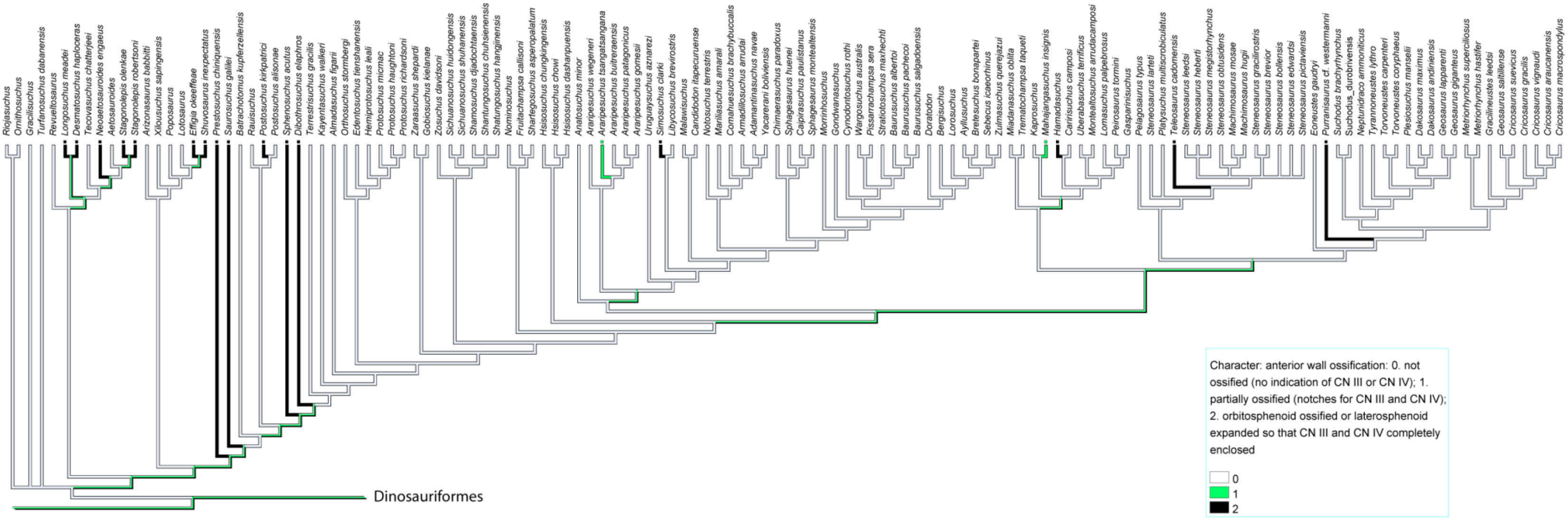

Figure 80: Optimization of character 11 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

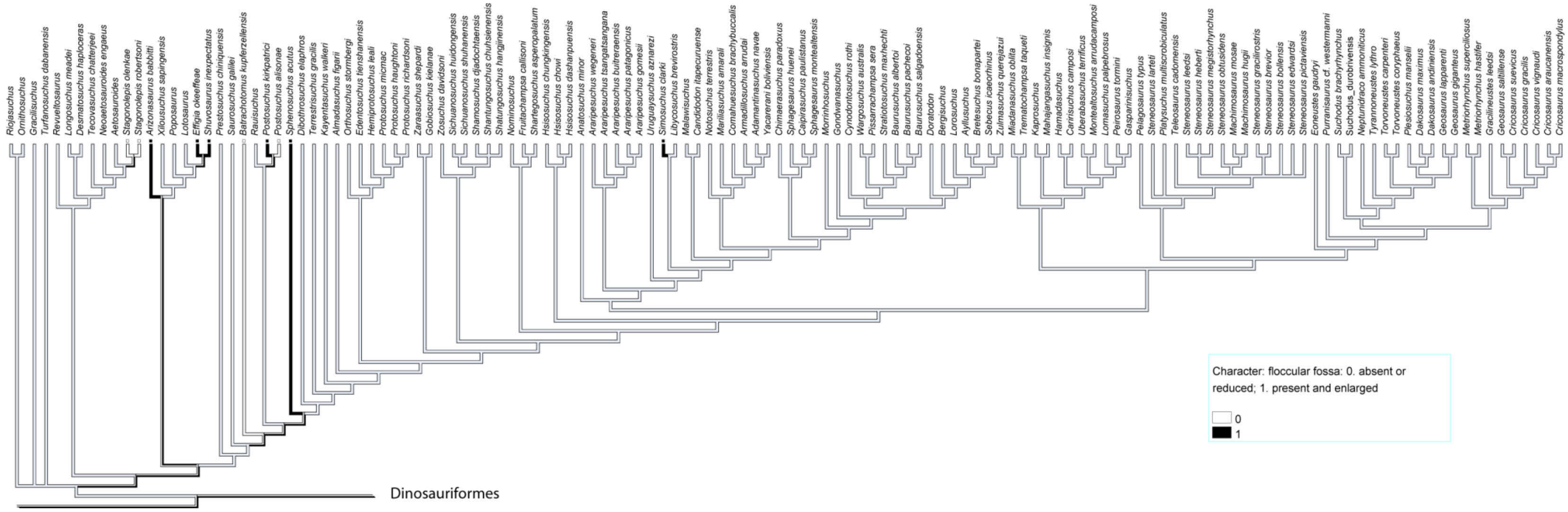

Figure 81: Optimization of character 14 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

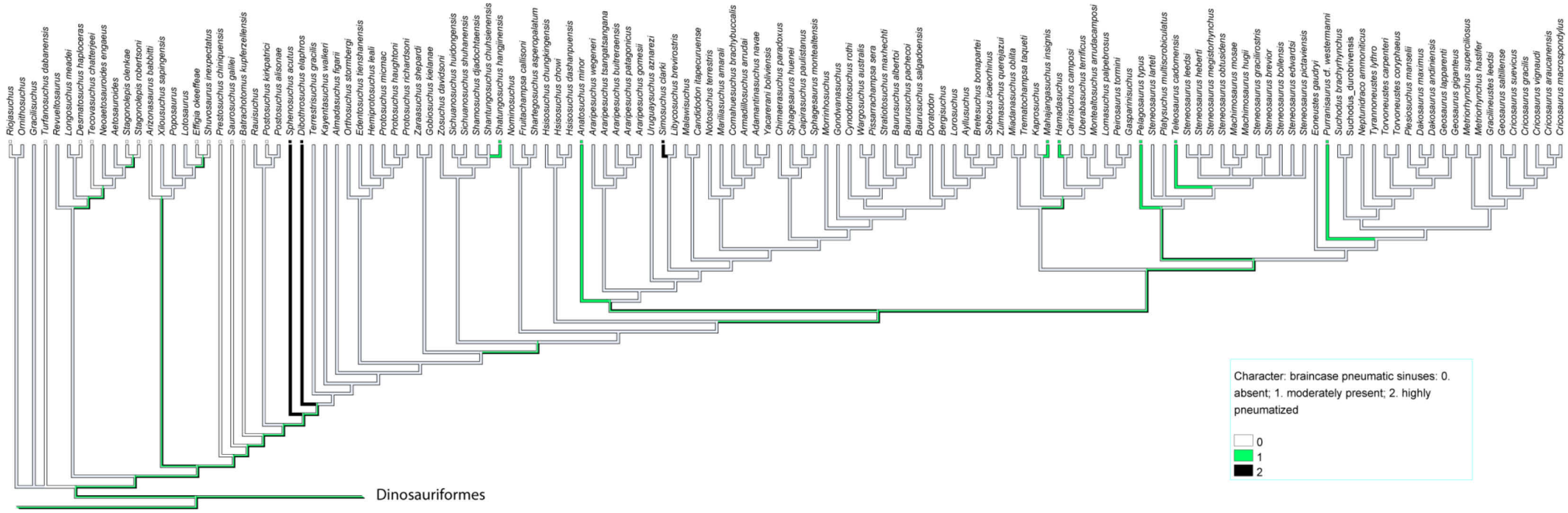

Figure 82: Optimization of character 15 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

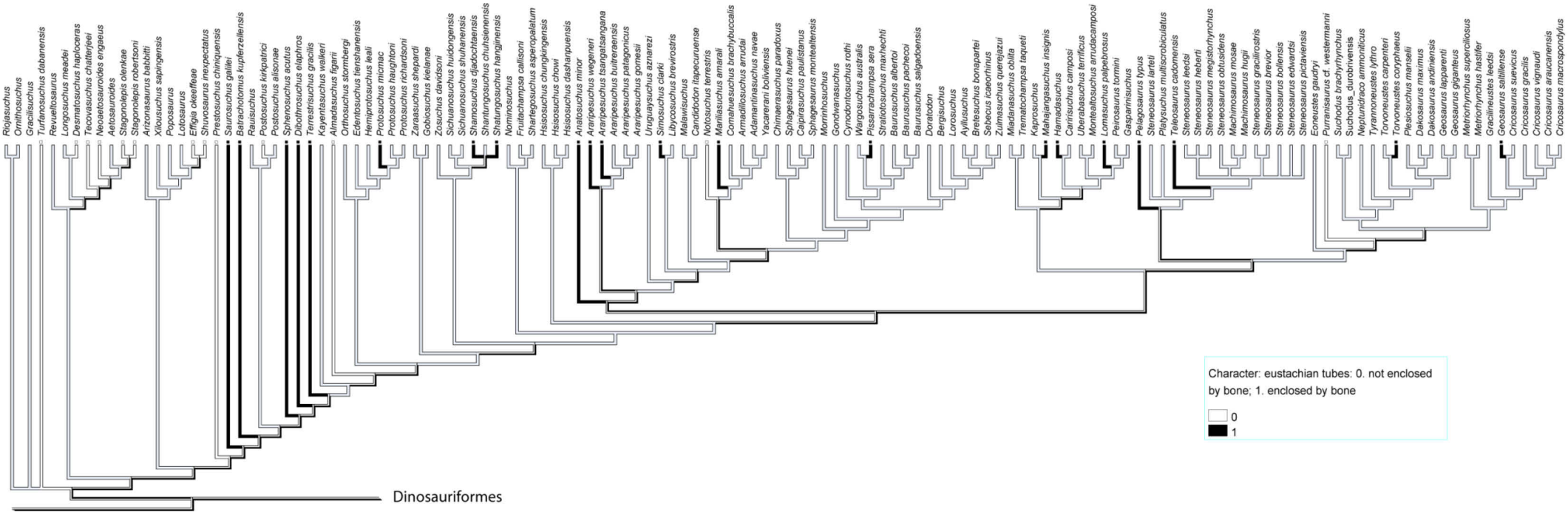

Figure 83: Optimization of character 16 for Pseudosuchia by likelihood. Please refer to figure for character definition and character states.

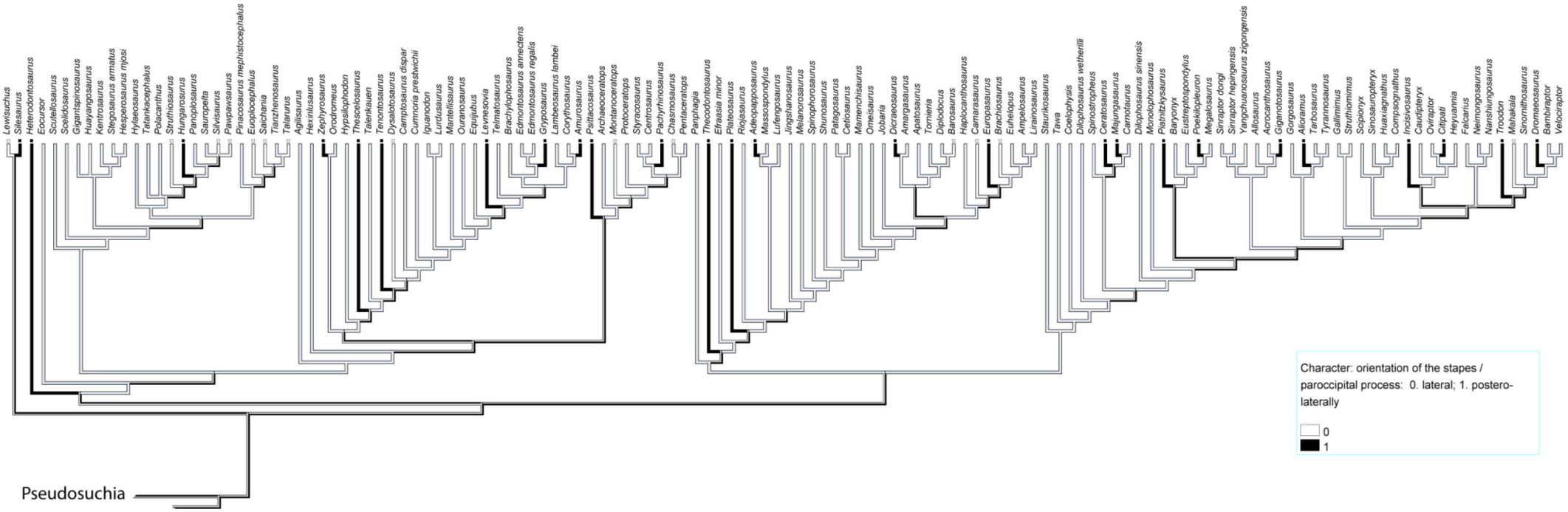

Figure 84: Optimization of character 1 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

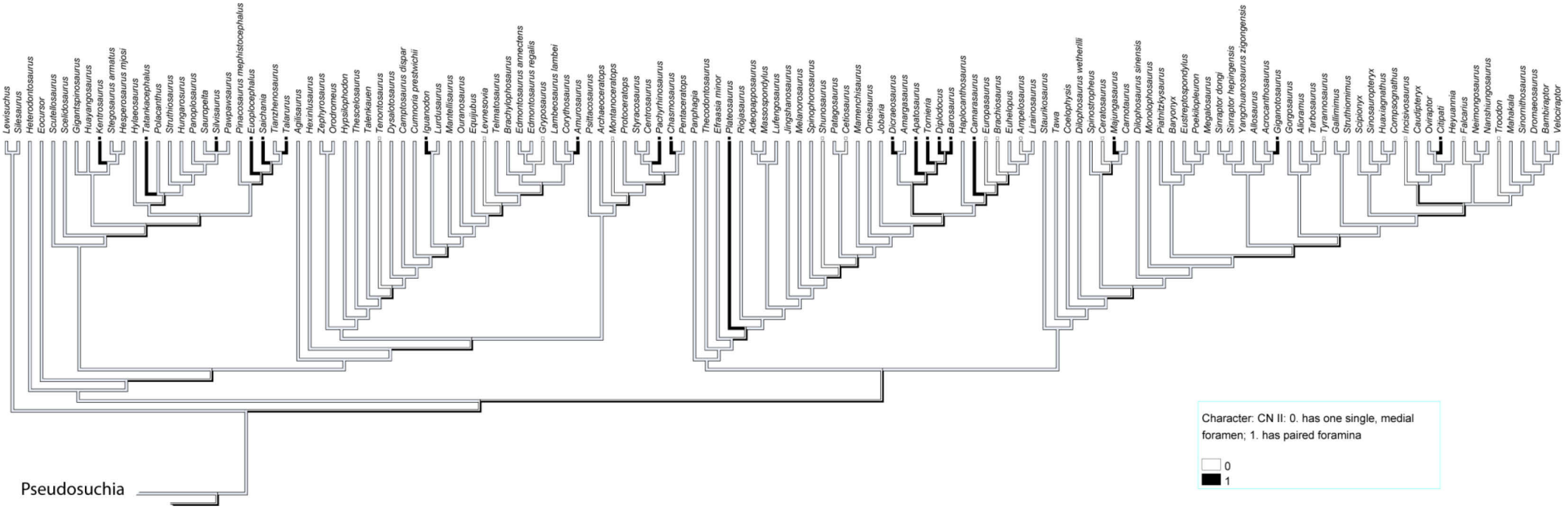

Figure 85: Optimization of character 2 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

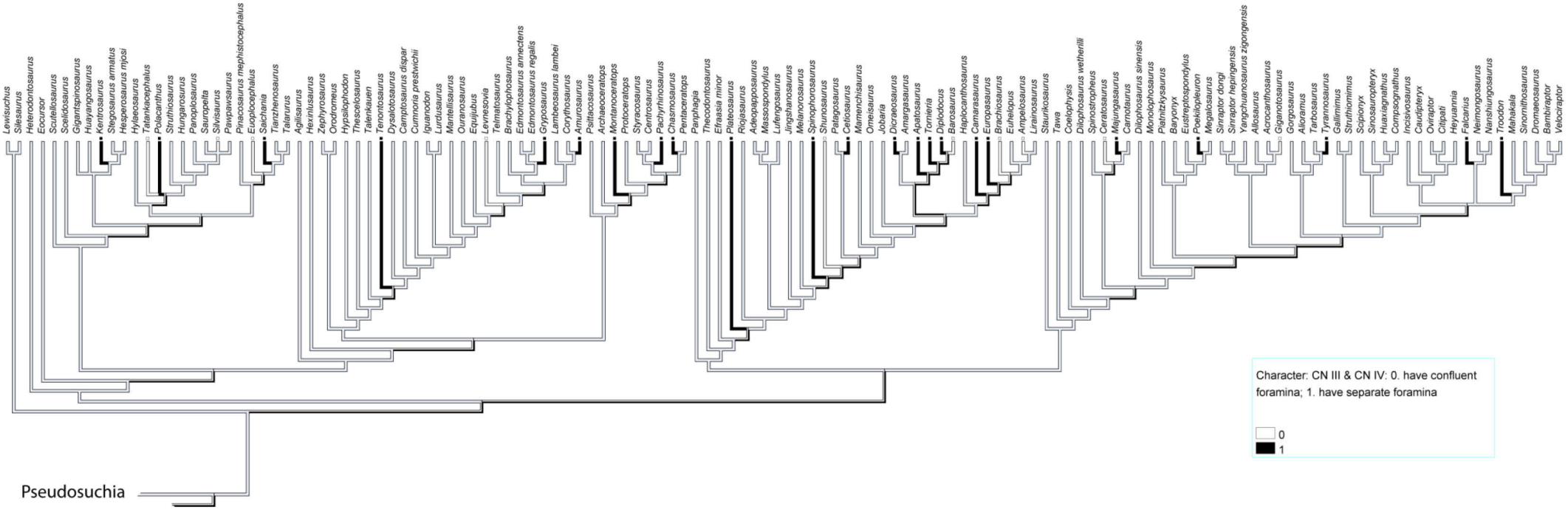

Figure 86: Optimization of character 3 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

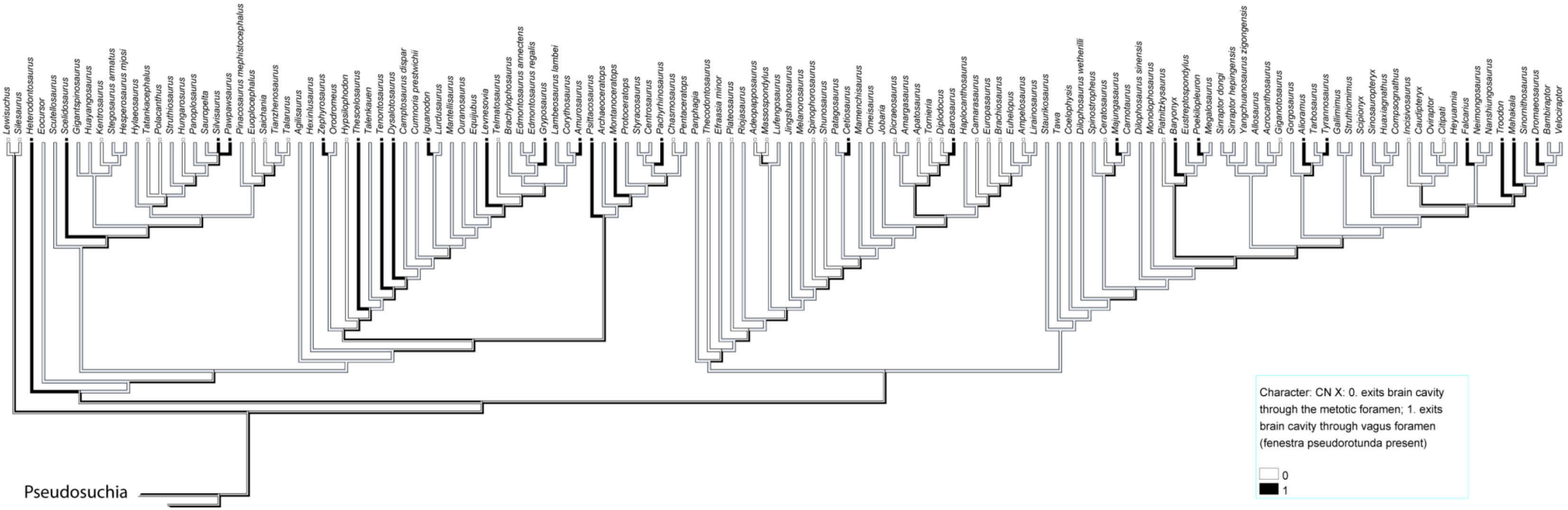

Figure 87: Optimization of character 7 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

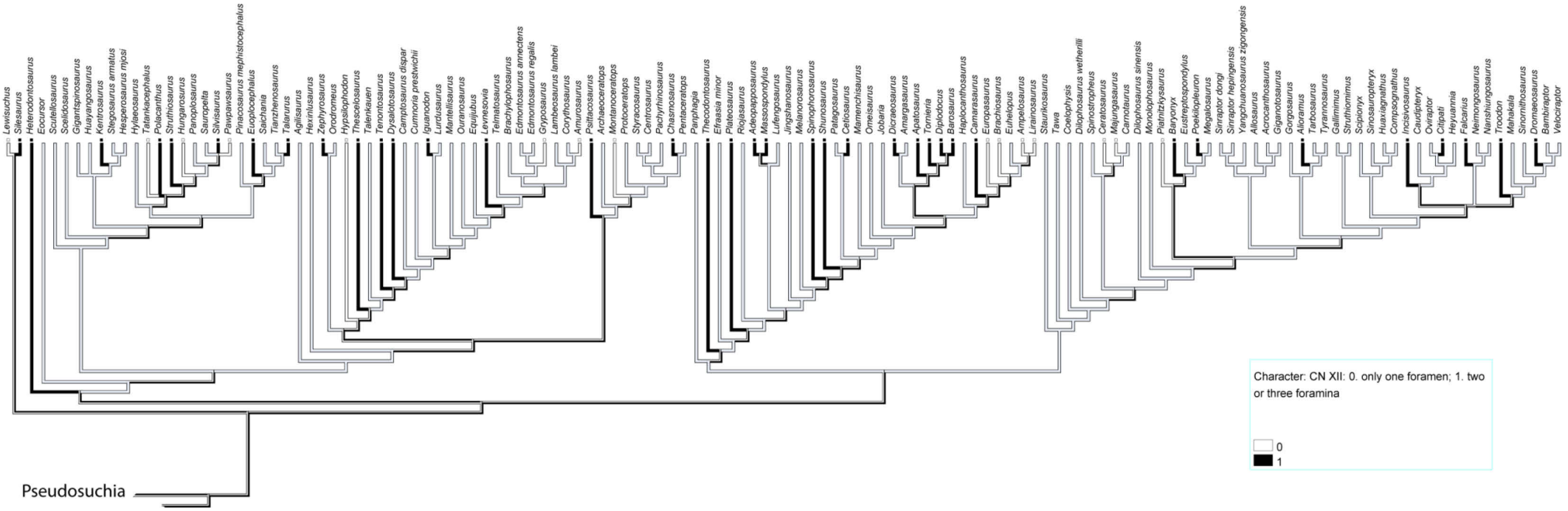

Figure 88: Optimization of character 8 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

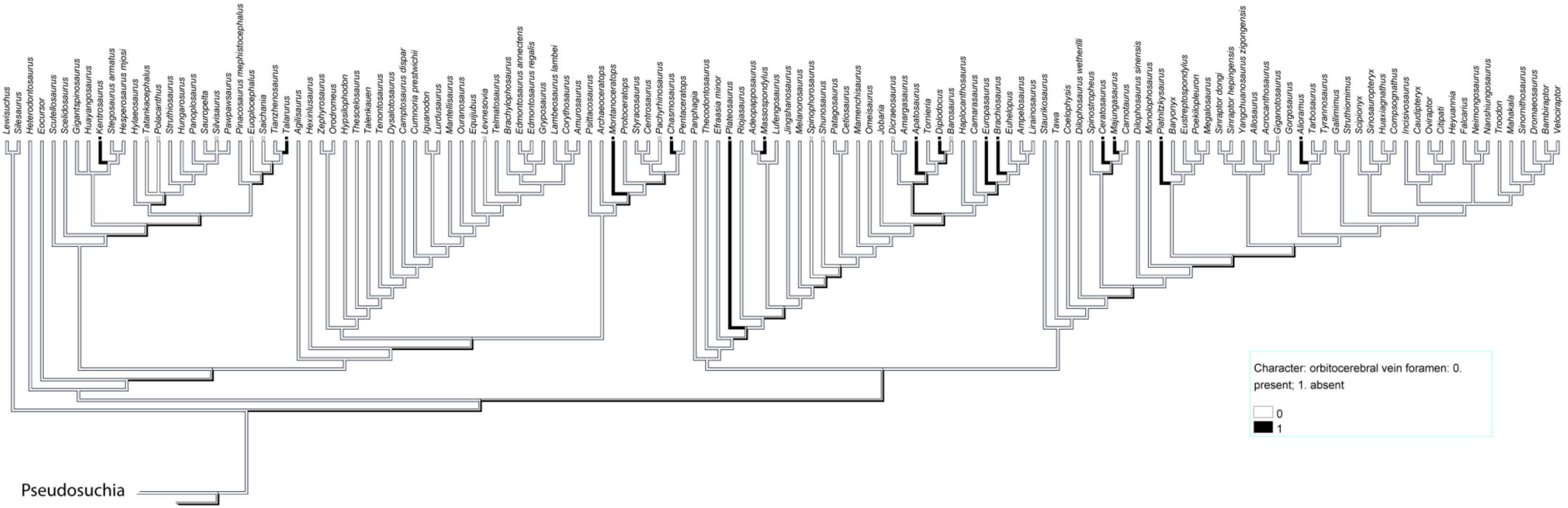

Figure 89: Optimization of character 9 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

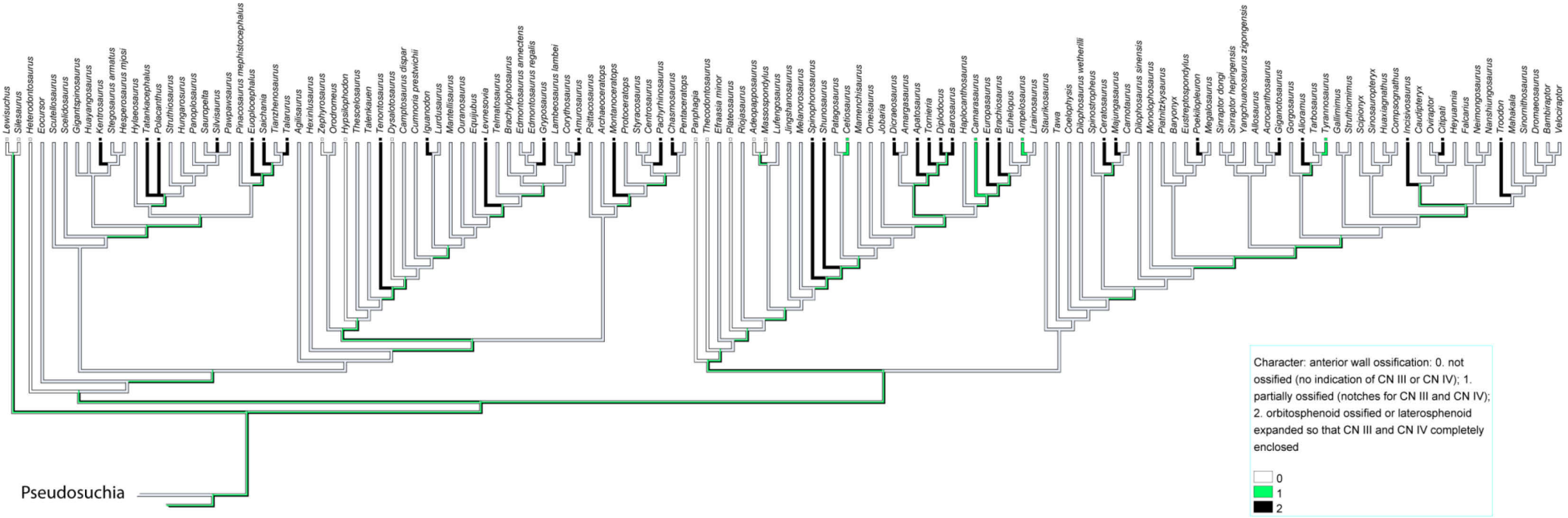

Figure 90: Optimization of character 11 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

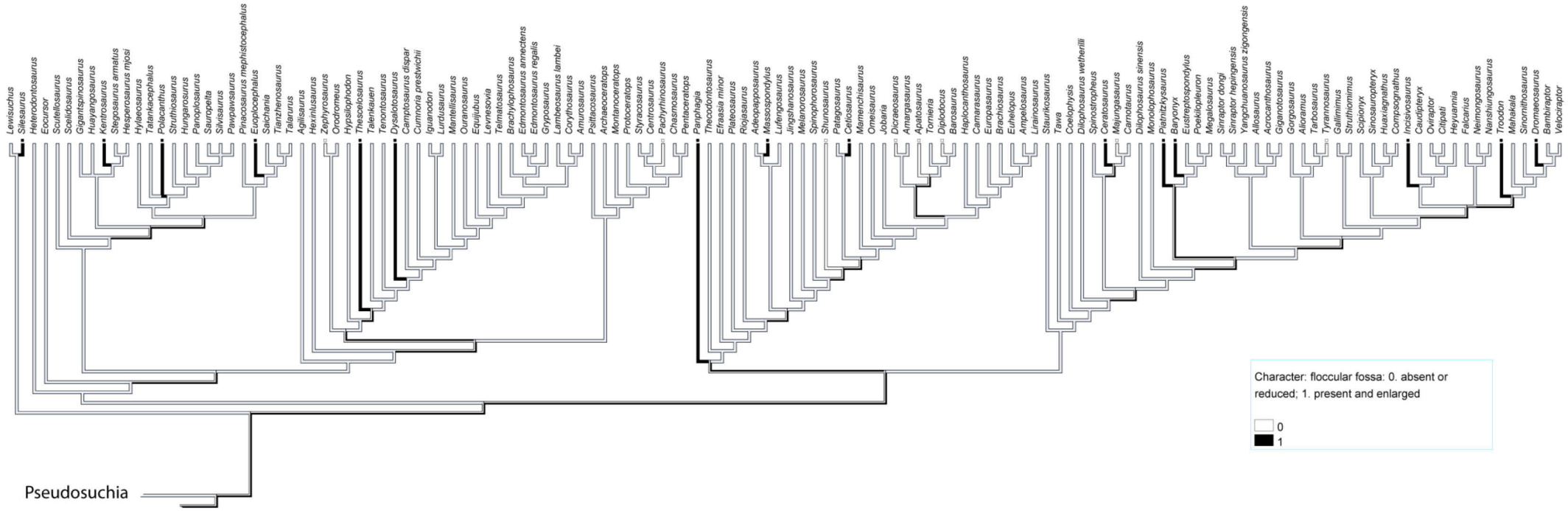

Figure 91: Optimization of character 14 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

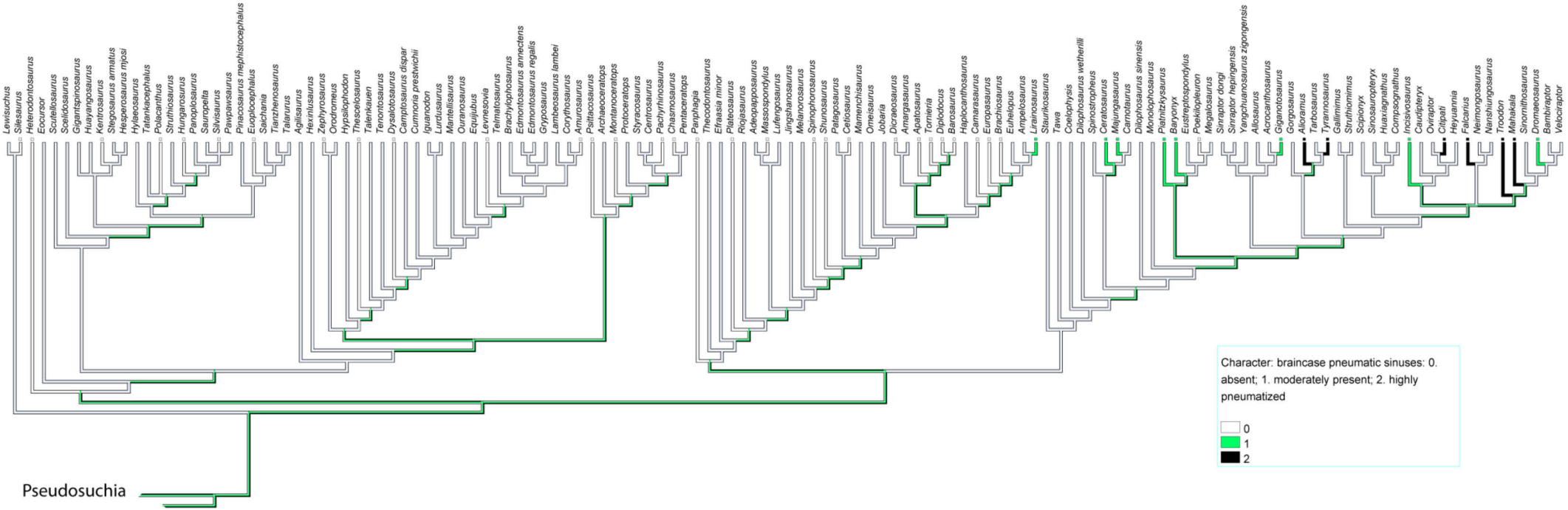

Figure 92: Optimization of character 15 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

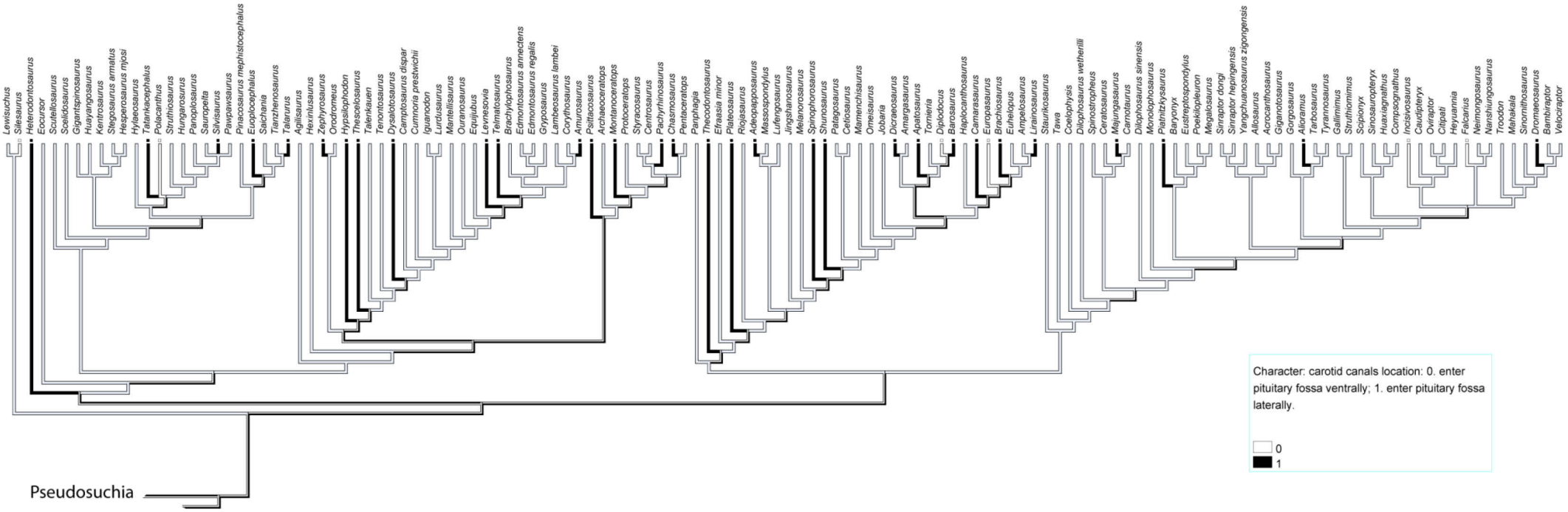

Figure 93: Optimization of character 17 for Dinosauriformes by likelihood. Please refer to figure for character definition and character states.

MACROEVOLUTIONARY TRENDS

The study of braincase anatomy of basal archosauromorphs and archosauriforms has given much insight into early braincase evolution, and helped fill the gap between more derived archosaur clades and diapsids. In general, there is a directional trend of the braincase ossifying anteriorly, with the expansion of the prootic and the ossification of the laterosphenoid in early archosauriforms and of the laterosphenoid in both archosaur clades independently. This may be related primarily with protection of the brain or development of specific musculature, but certainly has the important side effect of producing a more efficient acoustic isolation of the hearing system. The prootic and opisthotic develop ventrally, excluding the basisphenoid and basioccipital from the floor and rims of the fenestra ovalis and metotic foramen, decreasing the number of elements forming their borders. However this pattern may be not universal, since the non-archosaurian archosauriform *Euparkeria* shows participation of these elements in the referred fenestrae. There is also a trend in the development of the paroccipital process, with migration of its position to a more dorsal part of the braincase. The lateral braincase wall also exhibits development with the prootic, opisthotic and exoccipital all becoming dorsally expanded. The metotic foramen becomes markedly more developed in *Mesosuchus* and *Euparkeria*, and this might indicate an increasing selective force for the development of compensatory pressure-relief mechanisms and an improvement of the hearing system. In the non-saurian diapsid *Youngina*, the lateral semicircular canal is the longest, conforming with basal amniotes and tetrapods in general, but *Mesosuchus* and *Euparkeria* show development of the anterior semicircular canal, which is often regarded as reflecting developed motor skills, with precise movements and increased manoeuvrability, crucial for the survivorship in a more three-dimensional environment (Dudley & Yanoviak 2011, Sampson & Witmer 2007). This might relate to the adoption of a more erect posture of these taxa compared to diapsids with a sprawling posture. Additionally, when considering the braincase of more derived archosaurs such as the ornithischian dinosaur *Dysalotosaurus*, it becomes clear that arteries have very well defined paths and correlated anatomical features, whereas veins appear to be much more plastic and are therefore not reliable for assumptions of morphological homology (Sobral *et al*. 2012). Thus, we suggest the posterior foramen formed by the subdivision of the metotic foramen be called the vagus foramen instead of the jugular foramen, regardless of other elements that may have exited the braincase through it.

When the overall braincase morphology is investigated, it is clear that dinosaurs have the most plastic braincase morphology, showing the highest number of overall character state changes, with three times more changes than pseudosuchians (163 against 52). Within Dinosauria, those with a more plastic braincase morphology are the saurischians clades Sauropodomorpha and Theropoda, and the ornithischian clade Ornithopoda. On the pseudosuchian side of the tree, groups with the highest number of state changes are

Aetosauria, Notosuchia, and Thalattosuchia. In general, most of the changes occurring in braincase anatomy did not take place early in the evolutionary history of Dinosauria – neither temporally nor phylogenetically. By contrast, in Pseudosuchia, most state changes occur early in their history, during the Late Triassic and prior to the origin of Crocodyliformes. This reinforces the hypothesis for strong morphological constraint on braincase morphology that appeared with crocodyliform origin. Pseudosuchians were classically regarded as a group with a low morphological diversity, but contrary evidence has been growing and our results add to this high variability (Brusatte et al. 2008a, Stubbs *et al*. 2013). This is especially so in thalattosuchians, pelagic marine crocodylomorphs, which would be under even greater constraints due to their aquatic habits (Brusatte *et al*. 2008a, Brusatte *et al*. 2010b, Toljagić & Butler 2013, Stubbs *et al*. 2013). Notosuchians are the exception of this norm, as they are usually acknowledged as a morphologically and ecologically diverse group (Montefeltro *et al*. 2011, Stubbs *et al*. 2013), which seems to be reflected also in braincase anatomy. Therefore, it is noteworthy that thalattosuchians break many of the constraints imposed by the peculiar braincase anatomy of crocodyliforms, similar to notosuchians. Temporally, however, these state changes are not evenly distributed. Most of the dinosaur changes occur in the Late Jurassic (Sauropodomorpha) and Late Cretaceous (Theropoda and Ornithopoda), while pseudosuchian ones happen in the Late Triassic (Aetosauria) and Late Cretaceous (Notosuchia).

The majority of the shifts in diversification rates of dinosaurs take place temporally and phylogenetically early in the evolutionary history of the group, but pseudosuchian shifts are in general more evenly distributed in time and on the tree. Two of the pseudosuchian shifts, at the base of Notosuchia and at the origin of Sebecidae, had already been suggested as important radiation events for these groups (Pol *et al*. 2014). Furthermore, most of the pseudosuchian shifts occur in the main crocodilian line, but dinosaur shifts are concentrated mostly outside of the avialan lineage. Sauropodomorphs break the dinosaurian rule and have one of the shifts later in their phylogeny. Shifts occurring at the base of the theropod lineage confirm the decoupling of the origin of powered flight as a key innovation triggering diversification. Therefore, for saurischians, changes occurring in the braincase morphology might have played some role in the early diversification of theropods but not in sauropodomorphs. Also, for sauropodomorphs, an increase in body size is not correlated with braincase morphological diversity (Irmis 2010). This contrasts with pseudosuchians, and the Late Triassic shift of Crocodyliformes, this being the one with the highest number of character state changes. This additionally coincides with an increase in body size, suggesting a close relationship between phylogenetic and body size diversification. Using ancestral state reconstruction through parsimony, it is apparent that the most important dinosaurian shifts in terms of number of character changes are the ones in Thyreophroida

and Neosauropoda, both in the Early Jurassic. On the other hand, using a maximum likelihood approach, the most important shifts occur in Genasauria and Neotheropoda in the Late Triassic. Either way, it is worth noting that ornithischians usually have elevated correlation between shifts in diversification rates and character state changes, which suggests a trend that has not been previously detected. The shifts detected in Ornithischia concentrate at the base of more inclusive clades but are broadly distributed through time, and suggest overall steady morphological evolutionary rates. If, on the one hand, pseudosuchian character changes were fewer in number because of the constraint of the abutting of the quadrate and pterygoid against the lateral braincase wall, on the other these changes were frequently associated with shifts in diversification rates, highliting their importance to pseudosuchian evolution.

The results found in this analysis are compatible with an adaptive radiation scenario within Archosauria, as clade diversification occurs early in their evolutionary history, but not morphological diversification (Brusatte *et a*l. 2008a, 2010b). Braincases are a relatively rare component of skeletal remains and often they are not studied in great detail, hampering their potential usage in phylogenetic and macroevolutionary analyses. The situation is even more complicated for crocodyliforms, whose anatomy is frequently concealed by the lateral region of the skull and thus largely neglected. Developments in the application of computed-tomography scanning are expected to yield considerable insight into skull anatomy in future from fossils with previously inaccessible braincases.

IMPEDANCE-MATCHING HEARING

The fenestra pseudorotunda is not homologous for archosaurs. It appeared several times independently in dinosaurs (Figure 47), with reversals to an undivided metotic foramen, but it is likely that this only occurred once in pseudosuchians (Figure 46). Among dinosaurs, the character is more plastic in theropods. However, ornithischians were the first to develop this morphology in the Middle Triassic. Most of the appearances of this character, however, occur in the Late Triassic and Late Jurassic (Figures 94, 95), contrasting with the general trend of state changes of other braincase characters, which occur mostly in the Late Cretaceous. Impedance-matching hearing is overall not related to shifts in diversification rates, and is unlikely to have been a key innovation. However, it is associated with the diversification of Crocodyliformes and Thyreophoroida. In the case of ornithischians the shifts found are associated not only with some of the character state changes surveyed, but also with other published metrics of diversity, such as body size, supporting a multi-factorial diversification event for archosaurs. The appearance of the fenestra pseudorotunda is not correlated to the origin of buzzing and stridulating insect groups, suggesting that other selective forces must be acting on this character, such as intraspecific communication.

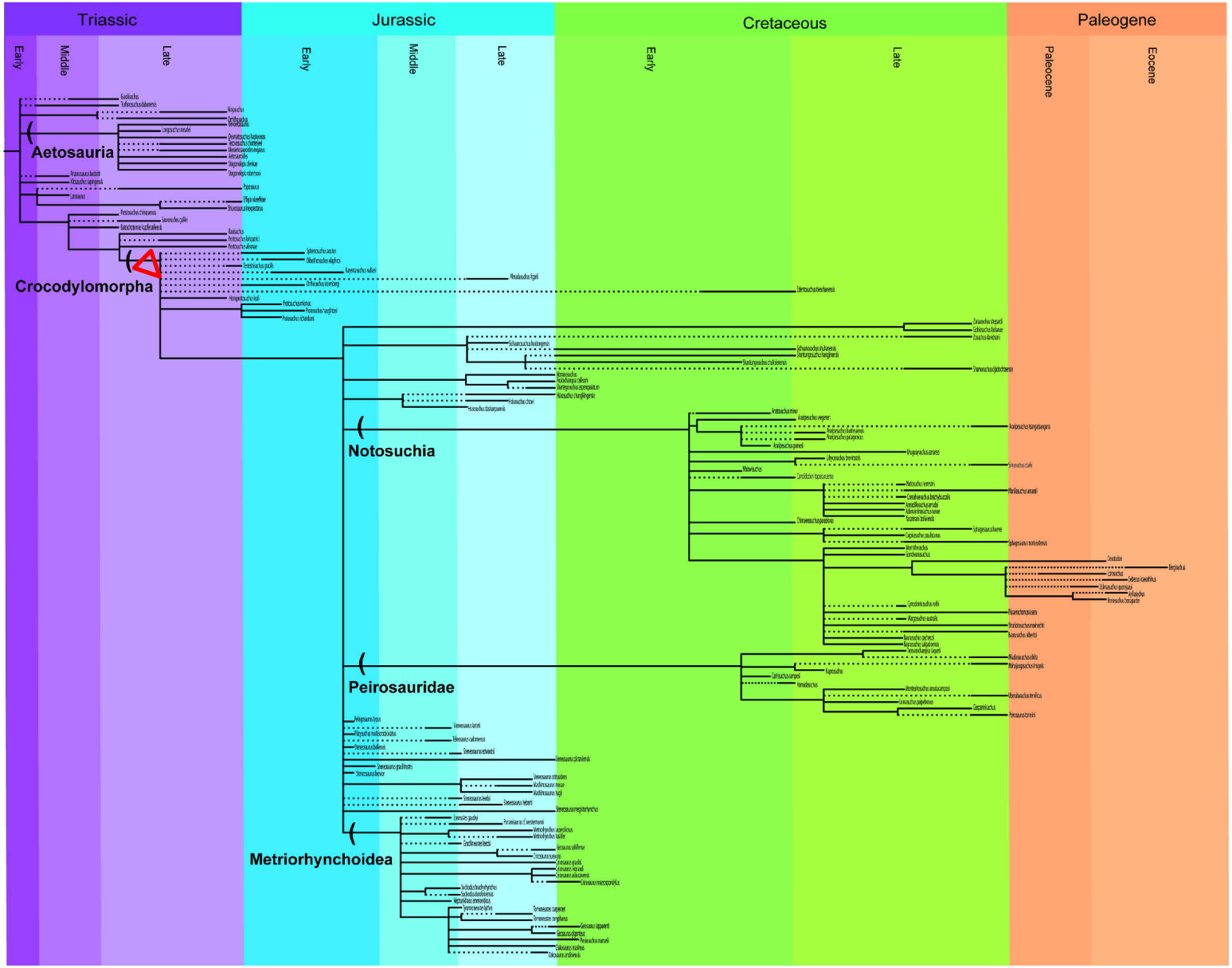

Figure 94: Temporal appearance of the fenestra pseudorotunda in Pseudosuchia (red arrow).

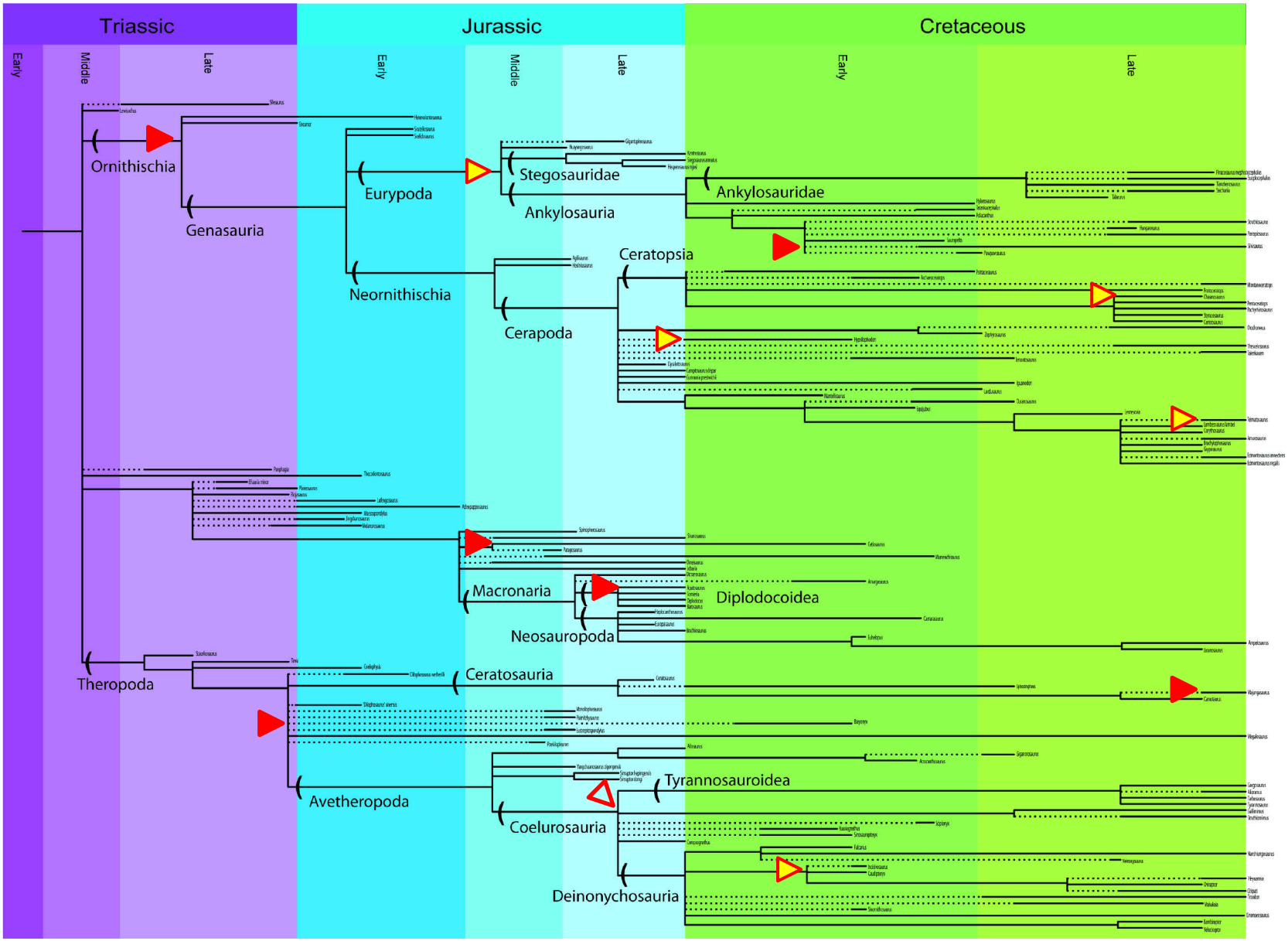

Figure 95: Temporal appearances of the fenestra pseudorotunda in Dinosauriformes (red arrows). Reversals are shown in arrows with yellow filling.

In a broader, amniote scenario, the presence of a fenestra pseudorotunda in archosaurs may be younger than for other groups. The sub-division of the metotic foramen occurred independently in Synapsida, and various clades within Squamata and Testudines. In squamates, the presence of a pressure-relief mechanism is reportedly plastic, and has been used as a phylogenetically informative character (Rieppel 1985). However, the hypothesis that these are all independent acquisitions has yet to be sufficiently tested. Nonetheless, the groups possessing a pressure-relief system have their origins in the Middle and Late Triassic (Clack 1997). Turtles, on the other hand, have been largely ignored with respect to the morphology of their braincase and otic regions, representing a potential future research area. Rieppel (1985) suggests this structure appeared in the Late Triassic only, but a convergence between cryptodiran and pleurodiran states much later in the Mesozoic has also been suggested (Clack 1997). On the other hand, it may be that the appearance of the fenestra rotunda in synapsids occurs at around the same time as in ornithischians. The braincase and middle ear of basal synapsids and cynodonts have similarly been largely ignored, but the metotic foramen of *Probainognathus* may have been internally and weakly sub-divided (Clack 1997). If so, then this feature appears in the Middle Triassic (Luo 2011), as with ornithischian dinosaurs. In contrast, the metotic foramen of the mammaliamorph *Adelobasileus* is definitely sub-divided, with this species dating from the Late Triassic (Lucas & Luo 1993), matching the hypotehsesised temporal appearance of the fenestra pseudorotunda in Crocodyliformes instead. Expanding this scenario and including all tetrapod groups is expected to provide further insights into the evolution of terrestrial hearing, and advances in phylogenetic comparative methods should provide a working framework for such an investigation. From the archosaurian pattern alone, however, it seems that impedance-matching hearing has no clear temporal or phylogenetically consistent pattern among groups. As such, different selective forces related to different environmental factors may be driving the development of this key factor in the evolution of sensory organs.

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